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Patterns in the distribution and abundance of terrestrial arthropods on sub-Antarctic Marion Island

by

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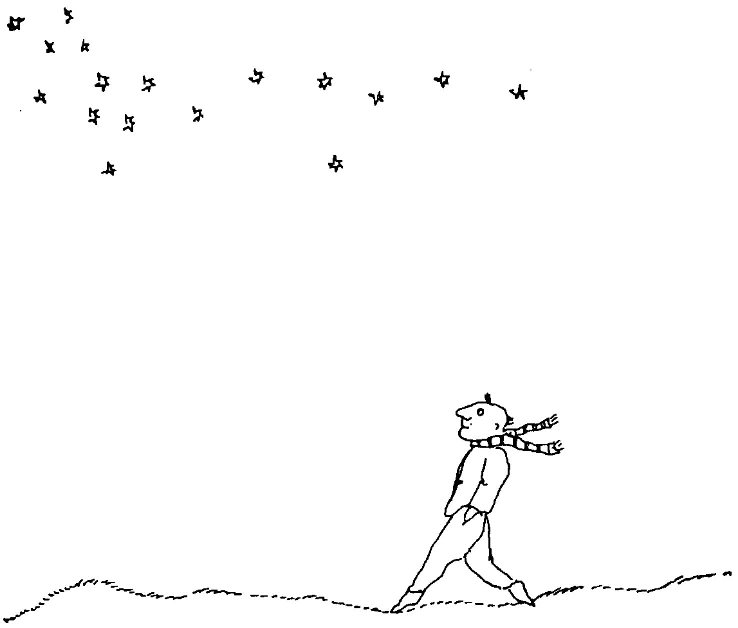

The Learn'd Astronomer

When I heard the learn'd astronomer,
When the proofs, the figures, were ranged in columns before
    me,
When I was shown the charts and diagrams, to add, divide, and
    measure them,
When I sitting heard the astronomer where he lectured with
    much applause in the lecture-room,
How soon unaccountable I became tired and sick,
Till rising and gliding out I wander'd off by myself,
In the mystical moist night-air, and from time to time,
Look'd up in perfect silence at the stars.

Walt Whitman

Dedicated to Mr Albert Ross, who showed me freedom.....

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On a personal note, my masters, to me, represents far more than a piece of scientific work. It represents three years of my life, in which I was exposed to new things, people, thoughts and ideas. I'm happy to say that I did learn from this and experienced positive growth in a number of areas. Some of the people I have met I hold dearly, and this makes the whole experience more valuable. I finally have to thank MY God for this complete adventure, all the opportunities and all that I have gained from this.

May the Southern Ocean stay wild and free.....

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Abstract

Quantitative studies of complete soil arthropod communities are considered essential if a thorough understanding of the structure and dynamics of soil faunas, and their likely response to anthropogenic environmental change, is to be gained. In practice, however, high species richness and poor taxonomic knowledge for most systems often hampers the acquisition of such information. In consequence, many studies resort to the use of higher taxa or more qualitative data. Sub-Antarctic terrestrial systems which are moderately diverse with well-known faunas allow us to bridge some of these problems. Two major terrestrial habitat types (or biotopes) are distinguished on sub-Antarctic islands, namely the epilithic and vegetated biotopes. These two habitat types differ in terms of current extent of vegetational cover and age relative to previous glacial events. The epilithic biotope includes the older habitats such as rocky shores and fellfields that have escaped glaciation, have little vascular plant cover, and is cryptogam-dominated. Quantitative data on the soil fauna of a fellfield habitat on sub-Antarctic Marion Island is used to illustrate the pitfalls associated with the qualitative approach. Fellfield is an important vegetation complex in the broad Antarctic region, and on Marion Island consists of both bare rocky areas and cushion plants. Soil arthropod communities in these two distinct habitat components were quantified over one year. Species richness was relatively high (42 spp.) and consisted almost exclusively of indigenous species, although abundances were lower compared with less extreme vegetation types in the sub-Antarctic. In general, arthropods either showed no pronounced seasonal peak in abundance, or a summer peak, although these patterns differed between habitat components within species, and between species. Quantitative analyses highlighted prominent differences between the two habitat components in arthropod community structure, despite the fact that most species were common to both of them. Qualitative analyses, in contrast, obscured these differences, while the use of higher taxa for analyses of seasonality resulted in abundant species generally masking the phenologies of less abundant ones. It is concluded that quantitative analyses of soil arthropod communities are essential if natural and anthropogenic changes in their structure are to be detected, monitored and understood.

Studies on sub-Antarctic insects have suggested that species inhabiting the epilithic habitats exhibit higher habitat preference or specificity and also a higher incidence of biotic interactions, such as competition, than those in vegetated habitats. The Acari, a more speciose but less well studied group than the insects, is used to independently test the aspect of habitat specificity. Seventeen different habitats or zones belonging to both the epilithic and vegetated biotopes were quantitatively sampled for mites over a one year period. These included a rocky shore, mire and non-mire lowland vegetation, and a mid-altitude fellfield. Species richness across all habitats was 39 spp., while rocky shore habitats showed higher abundances, but lower species richness, and a distinct fauna, to strictly terrestrial habitats. Multivariate analyses indicated that mite assemblage structure differed significantly between all different habitat types. However, most species in the terrestrial habitats (both epilithic and vegetated) were shared, suggesting that the epilithic fellfield, and especially its vegetated component (*Azorella selago* cushion plants) would have been suitable refugia during glaciation. The shoreline, due to its distinct fauna, seems a less likely refuge from which recolonisation of vegetated habitats could have taken place. Most species could be considered habitat generalists, although the epilithic habitats (shore and fellfield) had more habitat specific species than the lowland vegetated habitats.

Bothrometopus elongatus is one of four *Ectemnorhinus*-group species restricted to the epilithic biotope on the Prince Edward Islands. The biology of this species was examined over a full year at Kerguelen Rise, a mid-altitude fellfield site on Marion Island. *B. elongatus* adults eclose from April onwards, reaching maximum densities (*c.* 17 individuals.m^{-2}) in September. Females mature approximately three eggs at a time and these commence hatching in July. Larval eclosion reaches a peak in November, during which time larval densities are also highest (*c.* 153 individuals.m^{-2}). The larvae develop through six instars, which is within the range found for other *Ectemnorhinus*-group species. The high densities of *B. elongatus* in fellfield habitats, and its single, virtually discrete annual generation, make this species unusual among insects indigenous to the sub-Antarctic. The latter generally have low densities compared to other micro-arthropods, prolonged life cycles, and flexible life histories. It is suggested that the diversity of life histories found amongst the indigenous insects at Marion Island presents considerable potential for testing environmental effects on insect life histories. An overview of sub-Antarctic insect life history data suggests that the indigenous species, with generally prolonged life cycles, are at a disadvantage relative to introduced ones that have more rapid cycles and often complete several generations per year. This is reason for concern given rapid climate change at these islands.

Chapter 1. General Introduction

> Here, surrounding the island,
> there’s sea,
> but what sea:
> it’s always
> overflowing,
> says yes then no,
> then no again, and no,
> says yes in blue,
> in sea spray, raging,
> says no and no again.
> It can’t be still:
> It stammers “My name is the Sea”……
>
> **Pablo Neruda – Ode to the sea**

When discovered more than three centuries ago, the forbidding shores of the Prince Edward Islands did little to suggest their potential for scientific research. In the early years assessment of value was based largely on the presence of economic resources such as fur seals. In the late 1940s, when South Africa (then the Union of South Africa) annexed these islands, their strategic value was the principal consideration. Since then much scientific work (biological and other) has been carried out and today the full value of sub-Antarctic islands, such as the Prince Edwards, is adequately realised (Chown 1997). The very characteristics that define sub-Antarctic islands also make them prime areas for research of global relevance (Bergstrom & Chown 1999; Hänel & Chown 1999a, 1999b). These features will be briefly described for Marion Island.

Location and physical features

The Prince Edward Island group, located about halfway between South Africa and Antarctica, is one of the few extremely isolated archipelagos strewn around the Antarctic Polar Frontal Zone in the Southern Ocean. The group comprises the larger Marion (46°54’S, 37°45’E) and the smaller Prince Edward Islands (46°38’S, 37°57’E). These islands are typically sub-Antarctic, and apart from their localities differ from other terrestrial Maritime and Continental Antarctic habitats in terms of climatic and biotic features (Holdgate 1977; Block 1994). Based on their positions in the South Indian Ocean and biogeographical similarities, the Prince Edward Islands are grouped together with three other groups, Îles Crozet, Îles Kerguellen, and McDonald and Heard Islands into the South Indian Ocean Province (SIP) of sub-Antarctic islands (*sensu* Lewis Smith 1984).

Marion and Prince Edward Islands are the summits of two adjoining shield volcanoes of late Quaternary origin with an estimated age of about 250 000 years, though the cores of the islands may be much older (Kable *et al.* 1971; McDougall 1971; Verwoerd 1971). During its existence, Marion Island has been subjected to at least three glacial episodes, while Prince Edward Island seems to have escaped glaciation (Schalke & Van Zinderen Bakker 1971). The final glaciations on Marion Island correspond with the ultimate Pleistocene glaciation, which ended approximately 12 000 to 16 000 before present.

Steep cliffs dominate the 72-km long coastline of Marion Island and are only broken by a few boulder-, and two sandy or shingle beaches (de Villiers 1972). Inland, the island presents a mosaic of different lava types. Younger post-glacial black lava flows (15 000 ± 8 000 yrs) cover about 80% of the surface while grey lava flows of pre-glacial origin cover only small parts of the island (Verwoerd 1971). Numerous scoria cones dot the slopes that rise steadily to the peaks, the highest of which reaches 1230 m above sea level (a.s.l.).

Marion Island's climate is strongly influenced by the surrounding ocean and can be described as cool and hyperoceanic (see Schulze 1971; Smith 1987; Smith & Steenkamp 1990). Some dominant features are:

1) Low mean annual air temperature (*ca.* 5 °C) but with small diurnal (mean, 1.9 °C) and seasonal (4.1 °C) ranges.
2) Very high precipitation (>2000 mm per annum), mostly in the form of rain and distributed approximately equally throughout the year, although the late winter months (August to October) are marginally drier.
3) A high degree of cloudiness (annual sunshine duration *ca.* 30 % of the maximum possible; yearly mean radiation receipt at surface *ca.* 3.5 $\mathrm{kWm^{-2}\ day^{-1}}$ compared with 7 $\mathrm{kWm^{-2}\ day^{-1}}$ at the top of the atmosphere).
4) High relative humidity (annual mean screen value 83±2%).
5) Strong, predominantly westerly, wind with an average of 107 days *per annum* experience gale force (>55 $\mathrm{km.h^{-1}}$) wind blowing for at least an hour.

Although the climate of Marion may pose some extremes such as high rainfall and powerful winds, temperature fluctuations are remarkably moderate, compared to other Antarctic zones. This has lead to the sub-Antarctic being viewed as a relatively aseasonal environment (Convey 1996). However, there exist much local variation in terms of climatic severity, e.g. the west coast is far more exposed to westerly storms, and conditions become more inclement with increased altitude (Blake 1996).

Vegetation and glacial history

The plant communities of Marion Island has been described and studied more extensively than those of any other sub-Antarctic island (Block 1984; Huntley 1971; Gremmen 1981). The general vegetation type is tundra-like in appearance, but it differs from the Northern

Hemisphere biome in some marked ways, mostly due to climatic differences and the relative youth of the sub-Antarctic sites (Smith 1987).

The island possesses an extremely poor indigenous vascular fauna of only 24 species, attributable to extreme isolation, geological youth and the climate. Quite alarming is the 12 man-introduced aliens that have become established (see Hänel *et al.* 1998), and also the recent high incidence of alien plants being recorded (Gremmen & Smith 1999). Indigenous species have wide ecological amplitude and occur in many of the available habitats. Some alien species have been found in all major vegetation types and their ranges are expanding whilst changing the structure of native communities (Gremmen 1997; Gremmen *et al.* 1998; Gremmen & Smith 1999).

Cryptogams (mosses, lichens and liverworts) form an important component of vegetation with 79 species of mosses and 36 species of hepatics being found. Approximately 50 species of lichens have been recorded. Cryptogams are especially dominant in the non-vegetated biotopes (such as cliff faces and rocky areas) that are collectively termed epilithic biotopes (see Chown 1989). Vegetated biotopes only occur at elevations below 500 m a.s.l. and occupy about half of the island's surface area (Gremmen 1981; Hänel & Chown 1999a).

Gremmen (1981), in his definitive study, identified 41 plant communities on phytosociological basis at the association or sub-association level, which can be grouped into six major complexes:

1) The **salt-spray** complex in the form of herbfields dominated by the species *Cotula plumosa* and *Crassula moschata*. This complex is restricted to shore-zone areas strongly affected by wind-blown sea spray. On the west coast the belt of salt-spray vegetation extends up to 300 m inland, whereas on the east coast it is only found as a narrow zone along the tops of coastal cliffs.
2) The **biotically influenced** complex, which is affected by the trampling and manuring of animals. This complex contains a wide variety of communities, mostly found on the coastal zone near colonies of seabirds and seals. An example is *Poa cookii* tussock grassland. Inland, the influence of surface nesters and burrowing species is also manifested by the presence of communities belonging to this complex.
3) The **drainage line** (*Acaena magelanica – Brachythecium*) complex, which forms at mire and lowland slope sites and drainage lines, in areas with above or below surface water movement, such as stream banks.
4) The **mire or bog** complex, characteristic of poorly drained areas with accumulations of waterlogged peat, and dominated by grasses and bryophytes.
5) The **lowland slope** (fernbrake) complex dominated by the fern *Blechnum penna-marina* on well-drained inclines.

6) The **fellfield** (also called fjaeldmark or wind-desert) complex that forms in rocky areas strongly exposed to wind. At altitudes below about 500 m a.s.l. this complex possesses both vegetated and epilithic biotope components, the former dominated by the cushion forming dicot, *Azorella selago*. At higher altitudes the complex becomes purely epilithic and is dominated by cryptogams.

The most important factors affecting the distribution and occurrence of these complexes seem to be the soil water regime (notably water content and lateral subsurface water movement), the influence of salt spray, and biotic influence through trampling and manuring by seabirds and seals. These components together account for 65% of variation in species composition and cover. Another parallel gradient is the change from organic to mineral soil, which is associated with a trend from sheltered to strongly exposed conditions (Gremmen 1981).

It is thought that the present vascular vegetation is of post-glacial origin with some species probably having survived glaciation (see Chown 1990). Palynological evidence indicates that there was an amelioration of the climate on Marion Island following the last glaciation, during which time the present vascular vegetation was established (Scott 1985). Prior to this event there was little change in vegetation during the Holocene period, except for perhaps a succession from *Azorella selago*-dominated communities to mire communities. It is also though that current higher altitude biotopes (around the 600 – 750 m level), such as fellfield, may be very similar to the vegetation that existed in ice-free refugia at the height of glaciation. With the advent of more favourable conditions these refugia could have acted as sources from which vascular plants could disperse to other areas (Chown 1990). The old age of some epilithic biotope habitats and their geological background may explain the surprisingly high indigenous species richness observed, for example, in fellfield (Gremmen 1981). It may also make them valuable for comparison with younger vegetated biotopes.

Vertebrate fauna

Vertebrates have been relatively well studied on Marion Island, and some monitoring programmes have been running for several decades. Native vertebrate species consist of seals (three resident species) and birds (29 species). None of the birds are truly terrestrial (except for the lesser sheathbill *Chionis minor marionensis*) and simply use the island as a site for breeding, moulting and resting. The species include large numbers of penguins and albatross, smaller petrels and other seabirds. The birds do not interact directly with terrestrial ecosystems (except for sheathbills and kelp gulls *Larus dominicanus* that may prey on terrestrial invertebrates) and their influence is restricted to the manuring and trampling of vegetation around the coastal zone. This also applies for the two species of fur seal *Arctocephalus* spp. and southern elephant seals *Mirounga leonina* that are restricted to the coast (see Panagis 1985; Smith 1978). The introduced house mouse *Mus musculus* is commonly found in most vegetation types and is thought to have a profound impact on both plants and invertebrates through selective foraging (Smith 1987; Smith & Steenkamp 1990; Chown & Smith 1993; Huyser *et al.* in press). A further way in which vertebrates may impact on the terrestrial systems is by acting as transport agents for both plants and animals to the island (Gremmen 1981; Pugh 1997).

Invertebrate fauna

Marion Island hosts a fairly depauperate invertebrate fauna, which is dominated by arthropods. There are 30 insect species in total, of which 12 are naturalised aliens (Crafford *et al.* 1986; Hänel & Chown 1999a). Furthermore, there are more than 60 species of free-living Acari (Marshall *et al.* 1999), 16 Collembola (Gabriel 1999) and four species of Aranea (Lawrence 1971). Thus far, research has focused predominantly on macro-arthropods and on aspects of their life histories (Crafford 1984), biology (Crafford & Scholtz 1986; Crafford *et al.* 1986; Crafford & Scholtz 1987; Chown & Scholtz 1989) and physiology (Chown & Van Drimmelen 1992; Chown 1993a; Crafford & Chown 1993). The ecology of selected habitats such as the littoral zone (de Villiers 1976) and biologically influenced and vegetated areas (e.g. Panagis 1985) has also been examined. However, micro-arthropods (springtails and mites) which are the numerical dominant terrestrial invertebrates have been little studied to date.

Rationale and objectives of this thesis

The enormous potential held by Marion Island due to its unique position and conditions makes it attractive for goal-orientated research initiatives that go beyond the collection of routine monitoring data. In the case of arthropod communities, especially micro-arthropods, even intensive faunal surveys have, until recently, been neglected. For example, the number of known Acari has increased from an estimated 20 species (Crafford *et al.* 1986) to more than 60 (Marshall *et al.* 1999) after only about three years of extensive sampling.

The Marion Island Terrestrial Invertebrate Ecology (MITIE) programme attempts to use Marion Island as a model system for obtaining data that could shed light on the relationships between energy availability, species energy use, body size, population density and biotic interactions in an entire assemblage. This is being done by quantitatively sampling both micro- and macro-arthropod communities in representative terrestrial habitats, based on Gremmen's (1981) plant complexes. This thesis, although part of this greater programme, has a far narrower focus on an important epilithic habitat, a mid-altitude fellfield. To date, ecological studies on Marion Island and most other sub-Antarctic islands have been biased towards communities in vegetated angiosperm-dominated biotopes (Chown 1993b). Knowledge of epilithic habitats, given their glacial history, age and their dominance in exposed and higher altitude areas, is essential for a more complete picture of the island's terrestrial system. Also, structural and other similarities between fellfields from the sub-Antarctic, and the maritime and continental Antarctic (Gremmen 1981; Kennedy 1996) such as harsh environmental conditions (Ashton &

Gill 1965; Smith 1977; Davey *et al.* 1992) and considerable age, may make these the only directly comparable terrestrial habitats in the region (Chown 1993b). Therefore, an example of mid-altitude fellfield found on pre-glacial grey lava deposits on Kerguelen Rise, Marion Island, was subjected to methodical ecological sampling. The focus was on the distribution, abundance and densities of arthropods. The collection of such baseline data will not only yield information on the current state of arthropod communities, but will open up comparative opportunities with other terrestrial arthropod communities on the island itself, and across the region. The moderately diverse fauna in the sub-Antarctic means that complete communities can realistically be defined in a quantitative fashion. Furthermore, quantitative data can be invaluable for monitoring purposes, especially in the light of large-scale changes such as global climate change and increased human pressures on isolated islands (Bergstrom & Chown 1999).

The contents of this thesis can therefore be summarised as follows:

1) The distribution of arthropods in a mid-altitude fellfield habitat through space and time is examined and compared to available information from other habitats. Using this habitat as an example the importance of quantitative data in soil arthropod community studies is emphasised.
2) The acarid assemblages of all major habitats (ranging from a rocky shore, lowland vegetation complexes, to a fellfield) on Marion Island are compared using multivariate methods. The relationships between different habitat types based on these assemblages, and habitat specificity of the constituent species are examined. Possible factors determining the observed patterns are discussed.
3) The biology of an endemic weevil species, *Bothrometopus elongatus*, which is restricted to fellfield habitats on Marion Island, is examined. This weevil displays remarkably high densities in the epilithic biotope, and its life-cycle is compared to phenologies of other sub-Antarctic insects, and discussed in the context of the sub-Antarctic as an aseasonal region. Differences between the life histories of indigenous and alien insect species, and the impact of these in the context of climate change at the islands are also assessed.

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Chapter 2. The importance of quantitative analyses in soil arthropod ecology: lessons from and for the sub-Antarctic*

> You are never given a wish without also being given the power to make it true.
> You may have to work for it, however.
>
> **Richard Bach – Illusions**

Introduction

In a review undertaken 17 years ago, Usher *et al.* (1982) identified two significant areas in soil arthropod ecology where progress was needed. These were the study of complete communities, and a shift in focus from larger (insects) to smaller (mites and Collembola) arthropods. They also urged that non-quantitative faunistic surveys (i.e. presence/absence data) be replaced by quantitative community-based work. Since then, surprisingly little progress has been made in the study of soil arthropod communities on a quantitative basis. Many studies examine selected species only, or resort to the use of higher taxa because of a lack of taxonomic knowledge (Behan-Pelletier & Newton 1999). This is unfortunate because it may limit not only the inferences that can be made about community structure and dynamics of this significant component of biodiversity (Groffman & Bohlen 1999), but also the practical application of this information for purposes such as conservation, pest control, and monitoring. To date, however, few studies have examined the likely problems caused by qualitative as opposed to quantitative studies, mostly because systems are too species rich to do so, and the lack of taxonomic knowledge still represents a formidable bottleneck that can confound quantitative work considerably (but see Walter & Proctor 1998; Walter *et al.* 1998).

In an attempt to overcome some of these problems, it has been suggested that the study of simple, naturally occurring soil ecosystems, such as those found in the Antarctic, may contribute to the understanding of more complex systems. However, the relevance of such simple communities to the more complex systems from the rest of the world has been questioned (Usher *et al.* 1982; Block 1985; Block 1994). One solution to this dilemma is to study soil arthropod communities in areas with moderately diverse, well-known faunas. The sub-Antarctic islands in the Southern Ocean fulfil these criteria because they represent small, partially-open, temperate systems that are faunistically relatively well known (Greenslade 1990; Pugh 1993; Chown *et al.* 1998; Davies & Melbourne 1999; Marshall *et al.* 1999), with arthropods representing the dominant indigenous terrestrial animals (Block 1984).

An investigation of qualitative versus quantitative data collection and analyses of patterns in soil arthropod communities in this region may also provide insight into the effects of these

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two kinds of analyses on conclusions regarding the seasonality of the species constituting such communities. Recently there has been some debate on the nature of seasonality in this climatically unique region (Vernon *et al.* 1998), with some authors arguing that most life history responses to the seasons are flexible (Convey 1996a, 1996b, 1997a), while others have suggested that programmed responses, characteristic of invertebrates in other areas, may also be present (Danks 1999). Most of this debate has been centred on studies of insects (e.g. Meyer-Arndt 1984; Ernsting *et al.* 1995), while the more cryptic soil fauna has received little attention from a quantitative perspective (see West 1984; Convey 1996a). Investigation of seasonality may also be of further importance in the context of rapid climatic changes taking place at most of the sub-Antarctic islands, in synchrony with global climate change (see Bergstrom & Chown 1999), and the differential responses to these changes of indigenous as opposed to aggressively invading alien species (e.g. Ernsting *et al.* 1999; Barendse & Chown in press).

In this study we therefore investigate differences in conclusions regarding community patterns, arising from qualitative versus quantitative analyses of the distribution and abundance of both macro-and micro-arthropods in fellfield on Marion Island. Fellfield (also known as wind desert or fjaeldmark) is a terrestrial habitat widely distributed throughout the sub-Antarctic, and the only terrestrial habitat common to this region, the maritime Antarctic, and the continental Antarctic (Gremmen 1981; Chown 1993a). Hence, it is arguably the most significant terrestrial habitat throughout the broader Antarctic region, and one that is likely to be vulnerable (especially in terms of its areal extent) to climate change (see Chown 1990; Kennedy 1996; Frenot *et al.* 1997).

Materials and methods

Study site

The South African possessions of Marion (46°54'S, 37°45'E) and Prince Edward (46°38'S, 37°57'E) Islands form the Prince Edward island-group, one of the few isolated archipelagos scattered around the Antarctic Polar Frontal Zone in the Southern Ocean (Fig. 2.1). They are typical sub-Antarctic islands in terms of their climate, geology and biology (Smith 1987), and are distinguished from terrestrial Maritime and Continental Antarctic habitats (*sensu* Lewis Smith 1984) in terms of climatic and biotic features (Holdgate 1977; Block 1994). Within the sub-Antarctic region, Marion and Prince Edward Islands display biogeographical affinities to Îles Crozet, Îles Kerguelen, and McDonald and Heard islands (Chown *et al.* 1998), and belong to the South Indian Ocean Province (SIP) (Lewis Smith 1984). The study site at Marion Island was situated on Kerguelen Rise (see Fig. 2.1, GPS location: 46°55'17.8"S, 37°51'28.7"E), a typical, mid-altitude, grey lava fellfield area on the south-eastern side of the island (for detailed accounts of the topography and geology, see Van Zinderen Bakker 1971) with an elevation of about 250 m above sea level (a.s.l.).

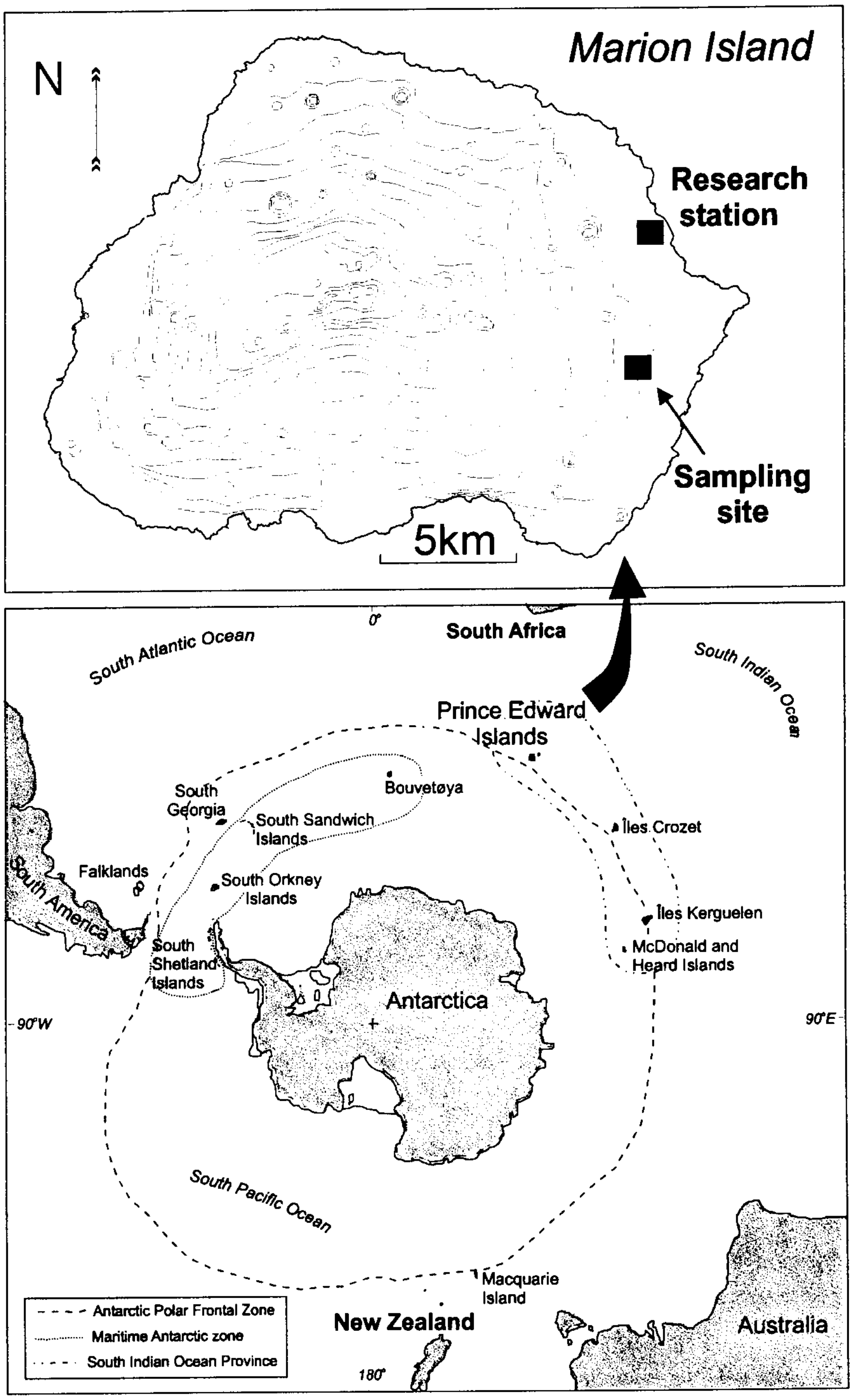

Figure 2.1 The location of the research station and fellfield study site on sub-Antarctic Marion Island and a map of the South Polar Region showing the island in relation to geographical and oceanographical features of this area.

The fellfield complex, one of six major vegetation community-complexes recognised at the Prince Edward Islands by Gremmen (1981), forms in rocky areas strongly exposed to wind. It is characterised by minimal plant cover, dominance by bryophytes, and decreased temperatures compared to lower lying areas (Gremmen 1981). Fellfield is thought to be the oldest of the community complexes on the sub-Antarctic islands (Chown 1994), and is a significant component of all the sub-Antarctic islands' lowland surface areas, while dominating at higher altitudes where it occurs on different substrata and with varying degrees of vegetational cover (Ashton & Gill 1965; Davies 1972, 1973; Gremmen 1981; Lewis Smith 1984; Selkirk & Seppelt 1984; Frenot 1986; Delarue 1988). Fellfield soils are loamy with large amounts of rock debris that can cover 40 - 100% of the surface. Compared to other soils where vegetated biotopes occur, fellfield soils contain little organic matter and have a low water content and low concentrations of plant nutrients (Smith 1977). A conspicuous component of the fellfields of the SIP islands is the cushion-forming dicot, *Azorella selago* Hook. f. (Huntley 1972; Gremmen 1981; Frenot *et al.* 1993). On Marion Island it can occur up to an altitude of 750 m a.s.l. above which cryptogams represent the only vegetation. Fellfield found in the sub-Antarctic, especially the high altitude variations, resembles and shares characteristics with the cryptogamic communities of the maritime Antarctic (Gremmen 1981; Kennedy 1996) and this structural similarity, common harsh environmental conditions (Ashton & Gill 1965; Smith 1977; Davey *et al.* 1992), and considerable age may make it the only terrestrial habitat directly comparable across the sub-Antarctic, maritime Antarctic, and perhaps even continental Antarctica (Chown 1993a).

Though fellfield is classified as a vegetation type (Gremmen 1981), it is clear that it supports little vascular vegetation. Accordingly, terrestrial habitats on Marion Island can be further classified into two major habitat types or biotopes, namely the vegetated biotope that is dominated by angiosperms, and the epilithic biotope which is cryptogam dominated (Chown 1989). The fellfield belongs to the latter, along with such habitats as rocky shores, lava outcrops and vertical rock faces (Chown 1992). For this study, *Azorella selago*, which occur as small islands (cushions) of closed vegetation in the mosaic of rocky debris of the fellfield, were considered to belong to the vegetated biotope along with other lowland vegetation types. The rocky areas in-between the cushions belong to the epilithic biotope (Chown 1989). Throughout this paper, "the fellfield habitat" is used as a collective term that refers to the vegetation type (after Gremmen 1981) including both vegetated and epilithic components. The "epilithic" component or biotope refers to the rocky, cryptogam dominated areas, while the "vegetated" component refers to *A. selago* cushions only.

Sampling programme

Two transects were chosen at the fellfield site. Because the two habitat components required different sampling approaches and because trampling resulting from sampling both components in a single transect could affect the other, each transect consisted of two adjoining, identical sub-transects (length 80 m) made up of four 20 x 20 m quadrats. One sub-transect was for sampling of the epilithic biotope component and the other for the sampling of *A. selago* cushions. As far as possible, sampling was conducted on days with favourable weather (no wind and rain). Sampling commenced in July 1997 and was carried out bimonthly up to April 1998 (the final two sampled months followed each other due to logistical constraints), thus a total of six month being sampled.

Cushions were sampled using an O'Connor split-corer (inside diameter of core = 70 mm and height = 70 mm; surface area ≈ 0.0039 m^2) (Southwood 1978; Edwards 1991). Only cushions with diameter ≥ *ca.* 15 cm were considered for sampling, because coring of smaller cushions proved to be too destructive. Ten cores were randomly taken from 10 numbered cushions in each quadrat during each sampling interval (i.e. 40 cores per transect per month and a total of 480 for both transects for the year). The same cushions was never sampled more than once. Half of the cores were extracted by Macfadyen high gradient extraction (extraction protocol: two days at 25 °C followed by two days at 30 °C, Macfadyen 1961) specifically targeted at micro-arthropods, while the other half was hand-sorted for macro-invertebrates (insects and earthworms, no micro-arthropods were collected). Due to their small size, data for *Apterothrips apteris* (Daniel) (Thysanoptera) obtained from high gradient extraction, and not hand-sorting, were used in the analysis. Earthworms were found in the hand-sorted cores, but data were not used for any analyses, as they were not efficiently extracted in the epilithic biotope, although they did occur there. Finally, the total number of *A. selago* cushions in each quadrat was counted. Individual *A. selago* cushions display highly variable shapes (Huntley 1972). Therefore, the approximate surface area of each numbered cushion was calculated as the product of the approximate length and width of each cushion (length was taken as the widest possible measurement of the cushion; width was the measure perpendicular to this axis).

The epilithic biotope was sampled by randomly taking five 30 x 30 cm samples from each of the four quadrats per month (i.e. 20 samples per transect per month and a total of 240 samples for both transects for the year). A sample consisted of the upper layer of loose rock and plant (i.e. mostly bryophytes) material scraped from within a 30 x 30 cm sampling grid down to no deeper than 10 cm. Because material was removed, a sample could never be collected from the same random position twice. Sampling was biased in that *A. selago* cushions and large boulders were purposely avoided, because the former were sampled separately and the latter could not be sampled using this sampling method. Arthropods were first extracted on-site by means of flotation in sieved (125 μm mesh-size) cold water from a nearby perennial stream. Water used for flotation was strained through 125 μm mesh first to prevent possible contamination. However, this was not done for July and sorting of these samples yielded many larvae of the aquatic midge *Limnophyes minimus* Meigen (Diptera), probably from the stream. Contamination of samples by this species is still not excluded as adults fly into buckets during washing and larvae may stick to the sides of buckets. This species was consequently excluded from our analysis of the washed samples. Samples were washed three times each, sieved through 125 μm mesh, and stored in plastic jars for transport back to the laboratory within six hours of collection. In the laboratory, further extraction of arthropods from samples was achieved by means of differential wetting (Southwood 1978) with kerosene and 70% ethanol (aqueous phase).

Finally, for both high-gradient and flotation samples, arthropods were separated by hand under a binocular dissecting microscope. Species were identified (insects: Crafford *et al.* 1986; mites: Krantz 1978; D.J. Marshall personal communication; Collembola: Greenslade & Gabriel, submitted manuscript) to the lowest possible taxonomic level and counted. This was relatively simple for the few, and taxonomically well known, insects and Collembola (Crafford *et al.* 1986; Gabriel 1999). However, because of numerous new records and undescribed species of mites (as recently listed by Marshall *et al.* 1999), their small sizes, the scale of the study, and the limitations of a dissecting microscope in identifying smaller cryptic groups (e.g. Prostigmata), identification down to species level was impossible in a few instances, and therefore families were used in analyses. Different life stages were not distinguished for species. All specimens were retained in 95% ethanol and are housed at the University of Pretoria.

Data processing and analyses

Raw counts for species were converted to densities per m^2 for all samples. Mean annual abundance (± standard error) per species and for higher taxonomic groups (Acari, Collembola and Insecta) was calculated, and species were ranked in order of abundance.

To test the effect of quantitative versus qualitative analyses on the interpretation of community patterns, data on mites from the two fellfield habitats and an additional, unrelated, lowland vegetated habitat, *Poa cookii* Hook f. tussock grassland (sampled in 1996/97 by A.G.A. Gabriel, see Gabriel (1999)) for a description of the O'Connor split core sampling, and high gradient extraction methods) were analysed using PRIMER v4.0 (Clarke & Warwick 1994). For the quantitative analysis (density data), a cluster analysis using group averaging and based on Bray-Curtis similarity measures was used to examine relationships between these three communities. Abundance data were double square-root transformed prior to analysis (in order to weight common and rare species equally). The same procedure was used for the qualitative analysis, but presence/absence data, with no transformation, were used. Furthermore, analysis of similarity (ANOSIM) was used to test for significant differences between these three terrestrial habitats (see Clarke 1993). This is a non-parametric permutation procedure applied to the rank similarity matrix underlying sample ordinations that calculates a global *R*-statistic. *R* values between zero and one it indicate some degree of discrimination between habitat types, the closer to one the higher the significance (Clarke & Warwick 1994).

Seasonal variation in abundance was only examined for the most abundant arthropods (mean annual densities of ≥ 10 individuals.m^{-2} (arbitrary benchmark, see Table 2.2), because the low numbers and high variance found in the remaining species precluded any decisive interpretation of temporal patterns. Accordingly, seasonality was examined for 27 different taxa. Because species were considered separately in each habitat component, but sometimes occurred in both, 41 cases of seasonality were examined. Different seasonal patterns in mean monthly abundance were identified according to whether and/or when (in terms of normal austral seasons, i.e. summer = Nov. to Jan., autumn = Feb. to Apr., winter = May to Jul. and spring = Aug. to Oct.) significant ($P < 0.05$) seasonal maxima occurred. This was done using Kruskal-Wallis analysis of variance (ANOVA) by ranks (data were found to be non-normally distributed). Significant peaks were identified with Dunn's multiple comparison test, a Tukey-type pairwise comparison (Zar 1996). Each observed seasonal pattern, or any other clear trend, was illustrated using one or more of the species displaying this pattern. Significance levels from Dunn's test were only reported for these chosen examples. To test the effect of the use of higher taxonomic groups on conclusions regarding temporal abundance patterns of the soil fauna, species were combined into their higher taxonomic groups (mesostigmatid, prostigmatid, and cryptostigmatid mites, and Collembola; astigmatids and insects contained only one species each per habitat component). The seasonal patterns of these groups were then examined, as is commonly done (e.g. Hijii 1987; Hutson & Veitch 1987; Al-Assiuty *et al.* 1993; Butterfield 1999).

Results

Community analysis

A total of 1028 *A. selago* cushions (including both sampled and not sampled) were present in both transects, and based on measurements of the sampled cushions (n = 480), a mean (± S.E.) surface area of 0.27± 0.0092 m^2 (max. ≈ 1.44, min. ≈ 0.045 m^2) per cushion was calculated. The cushions thus occupied 8.71% of the total surface area of this fellfield site.

With the exception of individuals belonging to one of the three mite families, Rhodacaridae, Nanorchestidae, and Tydeidae, or the aphids (Insecta), where more than one species might have been recorded in each family, all other higher taxa used are believed to contain a single species, even though the specific name may be unavailable (see Marshall *et al.* 1999) (Table 2.1).

Of the 30 established (that is, indigenous and introduced insects that have been recorded to breed, as opposed to transient aliens) macro-arthropod species recorded for the Prince Edward Islands (Crafford *et al.* 1986; Hänel 1999), 11 species were found here (Table 2.1). These include three naturalised alien taxa, *Apterothrips apteris*, *Limnophyes minimus*, and the aphids. Of the remaining eight species, all are endemic to Marion Island, except for *Antarctopsocus jeanneli* Badonnel (Psocoptera), *Halmaeusa atriceps* (C.O. Waterhouse)

(Coleoptera), and *Embryonopsis halticella* Eaton (Lepidoptera), which have wider sub-Antarctic distributions. Eight collembolan species, of a possible total of 16 recorded by Gabriel (1999) were found. These are all indigenous to the island with the exception of *Isotomurus* cf. *palustris* (Müller 1876), an introduced species (Gabriel 1999). Twenty-one mite taxa (probably more species) were recorded. It is uncertain how many of these species are introduced (see Pugh 1994, 1997).

Mites and springtails were numerically dominant (Table 3.2), with annual mean density reaching almost 16 000 individuals.m^{-2} in the case of *Eupodes minutus* (Strandtmann). Most insect species were represented by less than one individual per m^2. Although the two habitat components shared almost all species, these differed in density and abundance ranking between the vegetation and rocky habitat components (Table 2.2). Thus, there were considerable differences in community structure between the two fellfield habitat components. This is more apparent when a third terrestrial (vegetated) habitat, *Poa cookii*, is included in a cluster analyses, using mites only (Fig. 2.2). Using presence absence data only, the two fellfield habitat components were grouped together, whereas the quantitative analysis clustered together the two vascular plant habitats, to the exclusion of the epilithic fellfield component. Analysis of similarity between these three groups showed significant differences ($P < 0.05$) between all pairs of groups, in the case of both density and presence/absence data. However, the differences in grouping found between the two methods were at the 50% similarity level. Thus the faunistic survey suggested that there are major differences between the fellfield component and the *Poa cookii* grassland, whereas the quantitative analysis indicated that the community structure of the two fellfield habitat components are rather different.

Seasonality

Five major seasonality patterns were observed viz. summer, autumn, spring, and multiple abundance peaks, as well as a more aseasonal pattern (Table 2.3). The separation between these patterns was, however, not always clear cut. For example, some seasonal peaks were extended over a number of months. In such cases the pattern was categorised according the season where the highest abundance occurred, though the range of the peak is reported (Table 2.3). A species (or higher taxon) was placed in the multiple peak category when two or more abundance peaks occurred that did not differ significantly from each other. The aseasonal pattern was defined as one where no significant difference between the abundance of sampled months was detected by the Kruskal-Wallis ANOVA. In cases in Table 2.3 where a significant Kruskal-Wallis test statistic (*H*) reported, but the pattern is still classified as aseasonal, Dunn's test failed to identify a month that was significantly different from any other month.

Table 2.1 Complete species list of arthropods found in the mid-altitude fellfield habitat (after Lawrence 1971; Marshall *et al.* 1999; Crafford *et al.* 1986; Kuschel & Chown 1995, Hänel *et al.* 1998; Gabriel 1999).

Order / Suborder	Family	Species
	Mites	
Mesostigmata	Rhodacaridae	Gen.? spec.?
	Digamasellidae	*Dendrolaelaps* sp.
	Cillibidae	Gen.? spec.?
Prostigmata	Nanorchestidae	*Nanorchestes* sp.
	Eupodidae	*Eupodes minutus* (Strandtmann)
	Rhagidiidae	*Rhagidia* sp.
	Ereynetidae	*Ereynetes macquariensis* Fain
	Tydeidae	*Tydeus /Pertydeus* spp.?
	Bdellidae	*Bdellodes* sp.
	Stigmaeidae	*Eryngiopus* sp.
	Erythraeidae	*Balaustium* sp.
	Pygmephoridae	Gen.? spec.?
Cryptostigmata	Brachythonidae	*Liochthonius australis* Covarrubias
	Peloppiidae	*Macquarioppia striata* (Wallwork)
	Oppiidae	*Austroppia crozetensis* (Richters)
	Ameronothridae	*Halozetes fulvus* Engelbrecht
		Podacarus auberti Grandjean
	Oribatulidae	*Dometorina marionensis* van Pletzen & Kok
	Ceratozetidae	*Magellozetes antarcticus* (Michael)
Astigmata	Acaridae	*Schwiebea talpa subantarctica* Fain
	Algophagidae	*Algophagus* sp.
	Collembola	
	Onychiuridae	*Tullbergia bisetosa* (Börner 1902)
	Isotomidae	*Isotoma marionensis* (Déharveng 1981)
		Cryptopygus dubius (Déharveng 1981)
		Cryptopygus antarcticus travei (Déharveng 1981)
		Cryptopygus caecus (Wahlgren 1906)
		Isotomurus palustris (Müller 1876) group
	Neelidae	*Megalothorax* sp.
	Sminthuridae	*Sminthurinus tuberculatus* (Déharveng 1981)
	Insects	
Psocoptera	Elipsocidae	*Antarctopsocus jeanneli* Badonnel
Thysanoptera	Thripidae	*Apterothrips apteris* (Daniel)
Hemiptera	Aphididae	
Coleoptera	Curculionidae	*Ectemnorhinus similis* C. O. Waterhouse
		Ectemnorhinus marioni Jeannel
		Bothrometopus parvulus (C. O. Waterhouse)
		Bothrometopus elongatus (Jeannel)
	Staphylinidae	*Halmaeusa atriceps* (C. O. Waterhouse)
Diptera	Chironomidae	*Limnophyes minimus* Meigen
Lepidoptera	Tineidae	*Pringleophaga marioni* Viette
	Yponomeutidae	*Embryonopsis halticella* Eaton
	Spiders	
	Agelenidae	*Myro paucispinosus* Berland
	Linyphiidae	*Erigone vagans* Audouin

Table 2.2 Annual mean species abundance (expressed as mean density per m^2 ± standard error) with their ranks, in *Azorella selago* cushions (data for micro-arthropods from high gradient extracted samples and insects, except for *A. apteris*, from hand sorting) and the epilithic biotope ($n = 240$ for each type of sampling; ** denotes single record). Enchytraeid worms and earthworms were quantitatively extracted in the hand-sorted cores only, and are therefore included here for comparative purposes only.

	Annual mean density (individuals.m^{-2})			
Taxon	***A. selago* cushions**	**rank**	**Epilithic biotope**	**rank**
All mites	**1272.16±89.83**		**67.34±6.44**	
Rhodacaridae	723.23±61.23	11	24.17±3.79	10
Dendrolaelaps sp.	281.50±23.23	17	6.94±0.86	21
Cillibidae	651.78±68.96	14	117.50±9.87	5
Nanorchestes sp.	661.52±106.43	13	1.44±0.36	29
Eupodes minutus	15827.76±789.80	1	1.62±0.49	28
Rhagidia sp.	22.74±6.06 (23)	23	0.88±0.20	32
Ereynetes macquariensis	1183.37±79.72	10	0.56±0.17	34
Tydeidae	538.09±62.59	15	16.48±2.55	11
Bdellodes sp.	28.15±5.66	21	13.19±1.16	13
Eryngiopus sp.	4.33±2.15	26	6.62±0.75	22
Balaustium sp.	-		0.23±0.10	37
Pygmephoridae	31.40±8.37	20	1.94±0.51	27
Liochthonius australis	24.90±6.02	22	10.69±3.11	16
Macquarioppia striata	257.68±44.44	18	13.10±2.29	14
Austroppia crozetensis	4063.31±390.53	4	202.04±25.40	3
Halozetes fulvus	683.20±69.87	12	724.86±47.74	1
Podacarus auberti	18.41±9.81	24	0.14±0.08	38
Dometorina marionensis	401.68±52.07	16	238.84±25.41	2
Magellozetes antarcticus	2.17±1.53	28	25.37±8.18	9
Schwiebea talpa subantarctica	36.81±7.13	19	0.32±0.12	36
Algophagus sp.	1.08±1.08	31	7.08±2.12	20
All Collembola	**2881.5±188.56**		**38.22±4.82**	
Tullbergia bisetosa	4206.23±179.07	3	50.19±6.12	8
Isotoma marionensis	3683.29±347.01	5	147.92±16.65	4
Cryptopygus dubius	5979.66±350.46	2	10.42±1.88	17
Cryptopygus antarcticus travei	2747.85±139.77	8	62.78±7.27	7
Cryptopygus caecus	3220.99±199.22	6	6.11±1.27	23
Isotomurus sp.	5.41±2.40	25	10.93±1.31	15
Megalothorax sp.	2984.96±288.40	7	16.44±3.49	12
Sminthurinus tuberculatus	2.17±2.17	27	1.02±0.55	30
All insects	**153.80±27.60**		**12.10±1.00**	
Antarctopsocus jeanneli	-		1.99±0.48	26
Apterothrips apteris	1383.67±248.25	9	3.52±0.59	25
Aphididae	0.03±0.01	34	5.09±0.75	24
Ectemnorhinus spp.	0.30±0.05	32	1.02±0.26	31
Bothrometopus parvulus	0.03±0.02	36	0.56±0.19	33
Bothrometopus elongatus	0.07±0.02	33	98.24±6.09	6
Halmaeusa atriceps	0.02±0.01	39	0.49±0.15	35
Limnophyes minimus	0.03±0.02	37	9.86±1.33	18
Pringleophaga marioni	0.02±0.01	38	0.14±0.08	40
Embryonopsis halticella	**	40	-	
Myro paucispinosus	-		0.14±0.08	39
Erigone vagans	0.03±0.02	35	8.75±0.85	19
Earthworms	0.99±.10	30	0.23±0.10	37
Enchytraeid worms	1.17±0.12	29	-	

Figure 2.2 Dendrograms of cluster analyses of mite assemblages based on the Bray-Curtis similarity measure from three terrestrial habitats on Marion Island (Poa = *Poa cookii* tussock grassland; Epilith = epilithic biotope component in mid-altitude fellfield; Azo = *Azorella selago* cushions in fellfield; numbers and letters represent replicate sampling quadrats and transects). Dendrogram based on (**A**) presence/absence transformed data (qualitative) and (**B**) double square root transformed abundance (individuals.m^{-2}) data (quantitative).

Table 2.3 Seasonality patterns in abundance based on monthly mean density (individuals.m^{-2}) of the most abundant arthropod taxa in a fellfield habitat. Season (with month in brackets) of significant numerical peak ($P < 0.05$) as determined by Kruskal-Wallis ANOVA by ranks and Dunn's multiple comparison is shown. "Extended" refers to seasonal peaks with duration of more than a single month (the month with the highest abundance is given first, followed by the duration). "Multiple" refers to cases where two or more peaks occurred that were not significantly different from each other (month with highest abundance given first). Aseasonal pattern showed no significant difference ($P < 0.05$) between monthly means, or with pairwise comparison (Dunn's test) of months. Hyphen (-) indicates seasonality of species was not considered for that habitat. H = Kruskal-Wallis statistic.

	Seasonality pattern			
Taxon/Species	**Azorella -cushions**	*H*	**Epilithic biotope**	*H*
Rhodacaridae	multiple (Jan and Sept)	71.05	aseasonal	12.11
Dendrolaelaps sp.	multiple (Sept and Jan)	24.61	-	-
Cillibidae	multiple (Sept and Jan)	24.43	summer extended (Jan, Jan-Apr)	21.36
Nanorchestes sp.	autumn (Apr)	16.03	-	-
Eupodes minutus	summer (Nov)	45.81	-	-
Rhagidia sp.	aseasonal	11.16	-	-
Ereynetes macquariensis	autumn (Apr)	44.54	-	-
Tydeidae	summer (Jan)	38.22	multiple (Mar and Nov)	48.72
Bdellodes sp.	aseasonal	n.s.	autumn (Mar)	20.99
Pygmephoridae	aseasonal	n.s.	-	-
Liochthonius australis	aseasonal	n.s.	autumn (Apr)	45.58
Macquarioppia striata	aseasonal	n.s.	aseasonal	n.s.
Austroppia crozetensis	summer (Nov)	30.48	autumn (Mar)	22.46
Halozetes fulvus	summer (Nov)	72.12	spring extended (Sept, Sept-Jan)	67.56
Podacarus auberti	aseasonal	30.64	-	-
Dometorina marionensis	multiple (Apr and Nov)	21.31	autumn extended (Apr, Jan-Apr)	21.14
Magellozetes antarcticus	-	-	aseasonal	13.56
Schwiebea talpa subantarctica	aseasonal	18.55	-	-
Tullbergia bisetosa	multiple (Nov and Mar/Apr)	25.20	multiple (Apr and Nov)	30.71
Isotoma marionensis	multiple (Nov and Apr)	20.66	autumn (Apr)	45.53
Cryptopygus dubius	summer (Nov)	43.12	aseasonal	18.49
Cryptopygus antarcticus travei	autumn (Mar)	37.88	summer (Jan)	33.60
Cryptopygus caecus	autumn (Apr)	16.66	-	-
Isotomurus sp.	-	-	autumn (Apr)	23.53
Megalothorax sp.	aseasonal	n.s.	autumn (Apr)	45.24
Apterothrips apteris	summer (Nov)	153.9	-	-
Bothrometopus elongatus	-	-	summer (Nov)	47.45

The most commonly observed patterns in seasonality were summer peaks (Fig. 2.3A, Table 2.3) and the aseasonal pattern (Fig. 2.3B) with 13 cases each, followed by autumn peaks with 11 cases (Fig. 2.3C), eight cases of multiple peaks (Fig. 2.3D), and only a single spring peak (Fig. 2.3E). Although a few species had seasonality patterns that were similar across the two fellfield habitat components (Fig. 2.3F), most species showed different seasonal patterns between the two components. These included either a delay in peak abundance (Fig. 2.3G), or a completely different seasonal pattern. For example, the springtail *Cryptopygus dubius* (Déharveng) showed a summer abundance peak in the *A. selago* cushions, but an aseasonal pattern in the epilithic habitat component (Fig. 2.3H). The aseasonal pattern was most often found in species occurring at low densities and showing great variance in abundance (Tables 2.2 and 2.3) and this may suggest that the sample size was too small to detect seasonal patterns in these species. However, some species such as *Macquarioppia striata* (Richters) showed the same aseasonality in both habitats, although being much more abundant in the *A. selago* cushions (Fig. 2.3B), suggesting that the pattern was not artefactual.

There was generally a poor match between the seasonality pattern found for a higher taxon, compared with its constituent species. In the majority of cases, the most abundant species within a given higher taxon overwhelmed the pattern, and consequently seasonality patterns in the less abundant species were obscured (Figs 2.4A and B). In other cases, the most common pattern found in the composite species would dictate the seasonality of the composite species pattern (Fig. 2.4C), while still obscuring the presence of other, less common patterns.

Mean monthly temperature and total monthly precipitation (Stevenson Screen data) (Fig. 2.5), for the duration of the study, recorded at the Scientific Research station approximately five kilometres from the study site (see Fig. 2.1) are provided to show the small fluctuations in these climatic variables and apparent lack of seasonal cues.

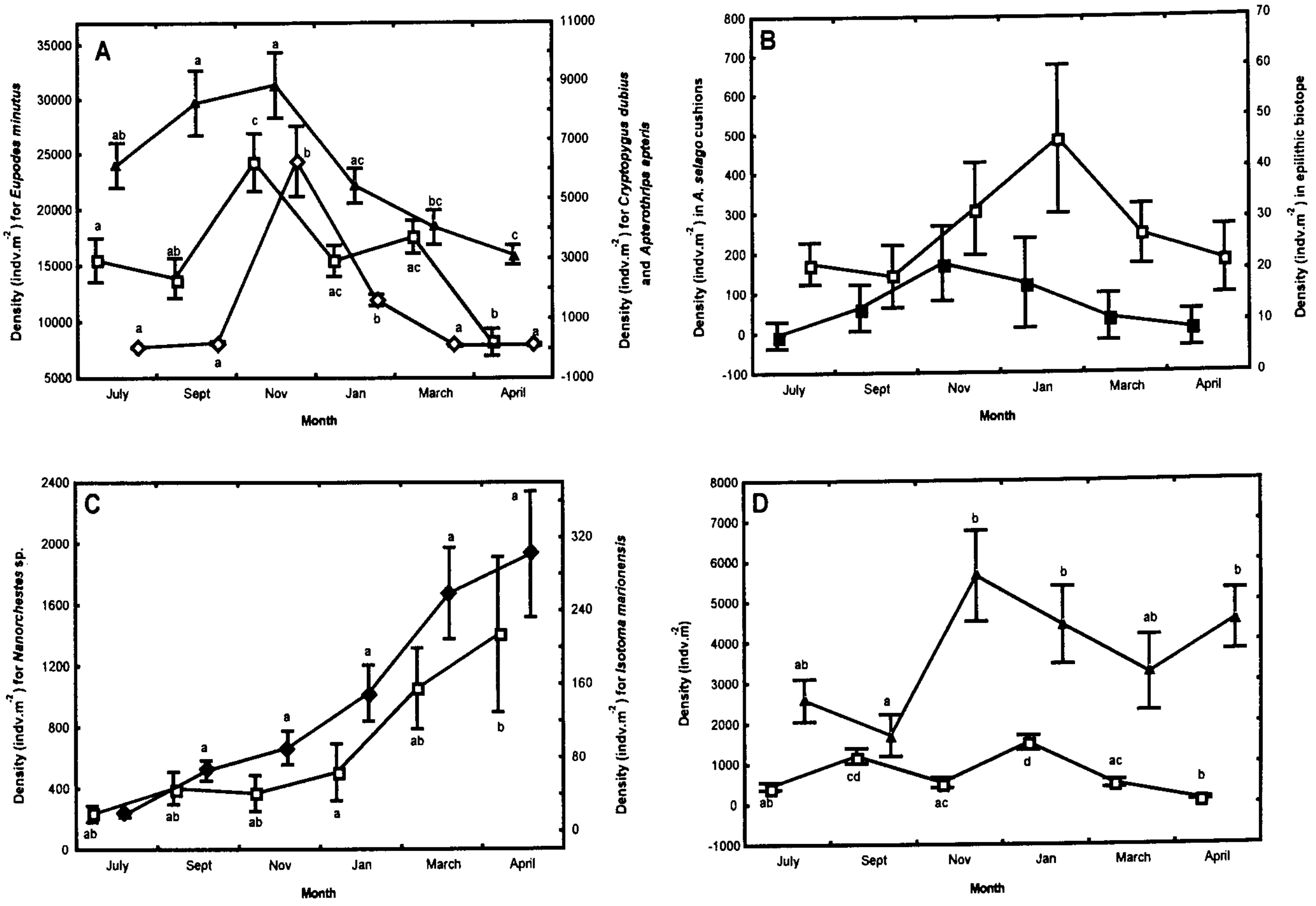

Figure 2.3 A – D. Seasonality patterns and features of selected arthropod taxa (also see Table 3.3) in the fellfield habitat on Marion Island. **Solid symbols always refer to the epilithic biotope and open symbols to *Azorella*-cushions.** Note the use of different scales for density in some cases. Identical letters at monthly means indicate no significant difference ($P < 0.05$) between these months, as shown by Dunn's multiple comparison. **(A)** Summer peaks in abundance (triangles = *Cryptopygus dubius*, diamonds = *Apterothrips apteris*, squares = *Eupodes minutus*). **(B)** Aseasonal pattern in abundance (squares = *Macquarioppia striata*). **(C)** Autumn peaks in abundance (diamonds = *Isotoma marionensis*, squares = *Nanorchestes* sp.). **(D)** Multiple peaks in abundance (triangles = *I. marionensis*, squares = Rhodacaridae).

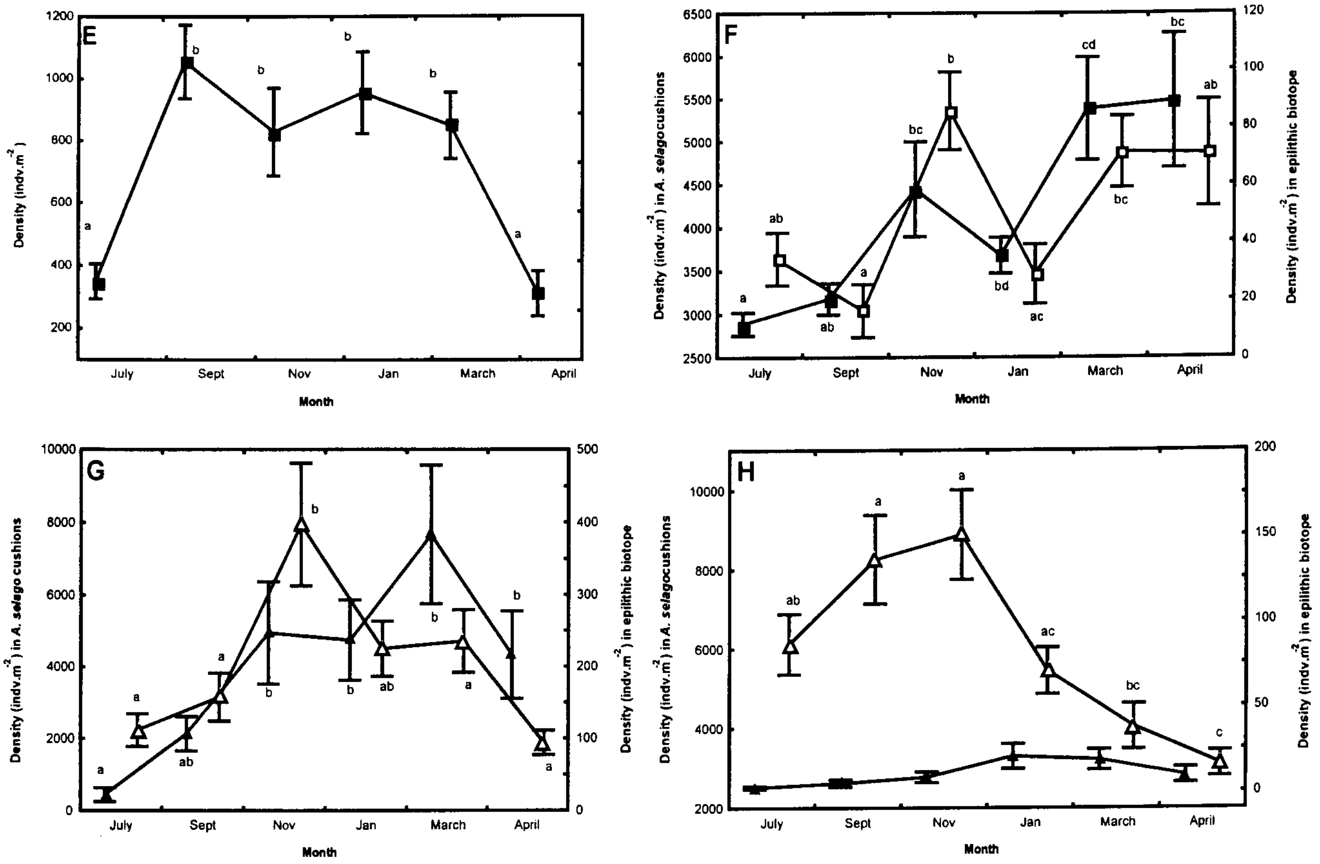

Figure 2.3 (cont.) E – H. (E) Spring peak in abundance for *Halozetes fulvus* in epilithic biotope (F) Similar seasonal pattern for *Tullbergia bisetosa* in both epilithic biotope and *A. selago* cushions. (G) Different seasonal abundance peaks for *Austroppia crozetensis* in epilithic biotope and *A. selago* cushions. (H) Different seasonal pattern for *Cryptopygus dubius* in two different habitat components, epilithic biotope and *A. selago* cushions.

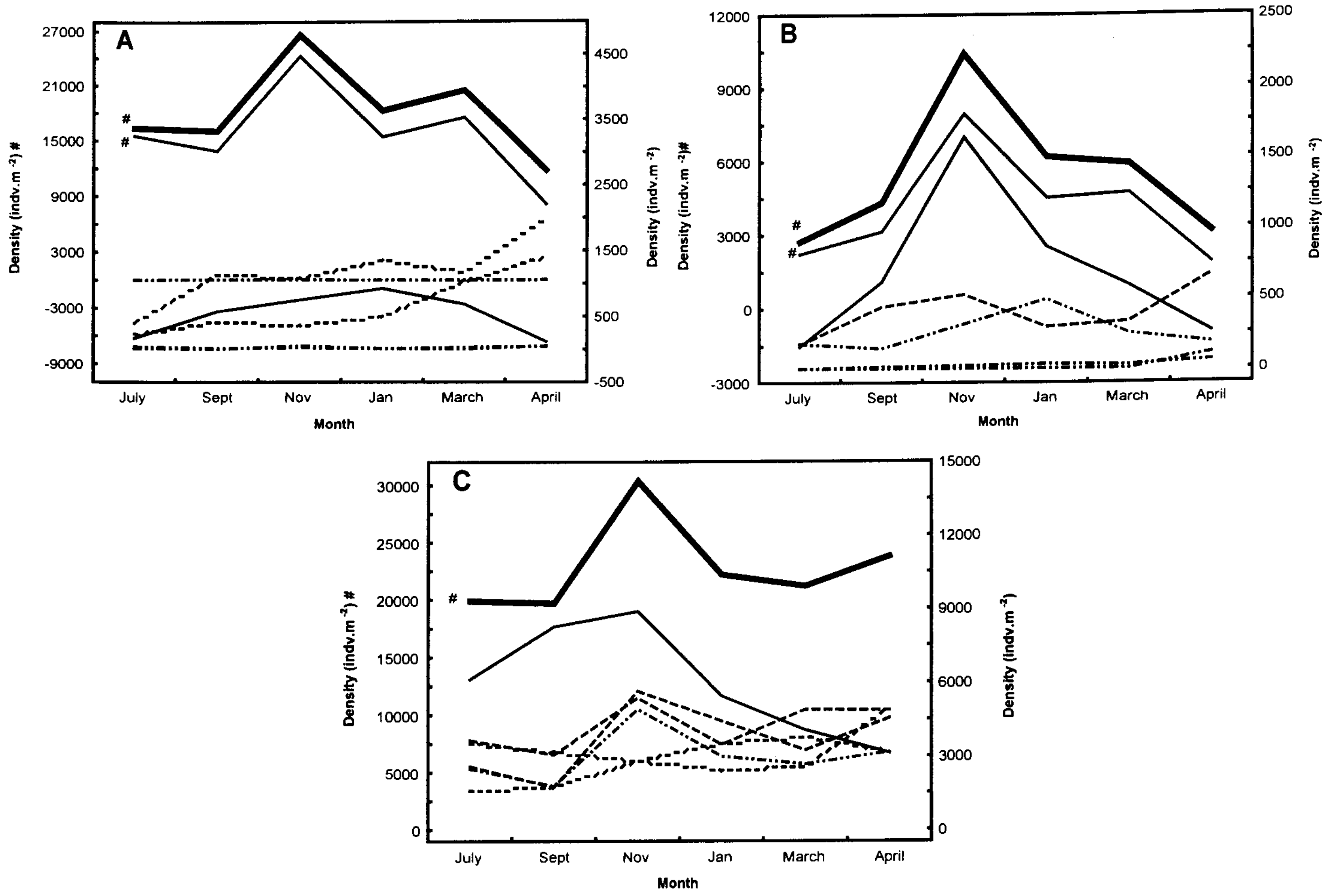

Figure 2.4 Seasonality patterns of three higher taxonomic groups (i.e. total monthly means of all species within a group) and their composite taxa, all in *Azorella selago* cushions in a fellfield habitat on Marion Island. Bold uppermost line represents cumulative pattern of the higher taxonomic group. Note that some plots are plotted on different scales, # indicates the relevant axis. (**A**) Prostigmata; (**B**) Cryptostigmata; (**C**) Collembola. Seasonality patterns: solid line = summer peak in abundance; dashed line = multiple peaks; dotted line = autumn peak; dash-single dot = spring peak; dash-double dot = aseasonal pattern.

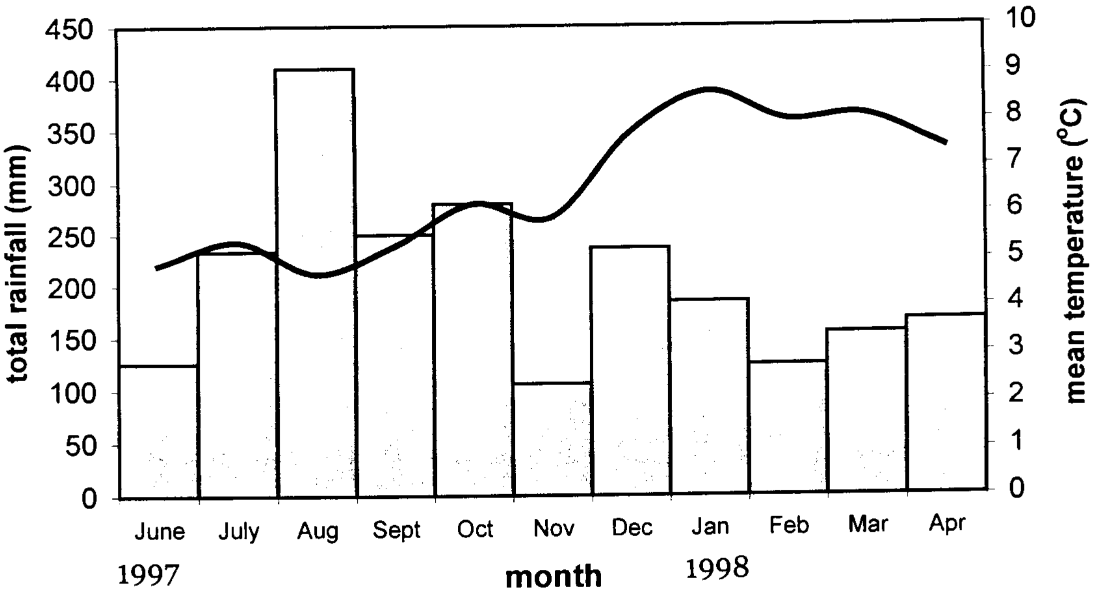

Figure 2.5 Stevenson Screen climatic data (total monthly precipitation in mm, and mean monthly temperature in °C) recorded at the research station during the study (Data from South African Weather Bureau).

Discussion

Community structure

As in most other soil habitats world-wide (see Behan-Pelletier & Newton 1999), mites (especially Cryptostigmata and Prostigmata) and springtails were the numerically dominant arthropods in the fellfield. However, with one or two significant exceptions, densities, especially those recorded in the epilithic habitat component, were generally low compared with those reported from low altitude vegetated habitats on Marion Island (Gabriel 1999; Barendse, Gabriel, Chown & Marshall, unpublished data), and from other sub-Antarctic, maritime Antarctic, and locations at a variety of latitudes (Goddard 1979; Block 1982; Block 1984; Peterson & Luxton 1982; West 1982, 1984). On the other hand, arthropod species richness in the fellfield habitat was high compared with that of habitats in the low altitude vegetated biotope on the island (see Crafford *et al.* 1986; Gabriel 1999; Hänel 1999; Marshall *et al.* 1999). High insect species richness in fellfield compared with vegetated habitats has been recorded previously both for Marion Island and for the sub-Antarctic as a whole (see Davies 1973; Chown 1989, 1990), and is thought to be a consequence of the greater age of the former habitat (Chown 1994).

The lower abundance and relatively high species richness displayed by the Marion Island fellfield supports the idea that sub-Antarctic and other Antarctic fellfields share many characteristics. Lower abundance and activity of micro-arthropods have been found in fellfield habitats on Signy Island and is thought to be the consequence of harsher abiotic conditions in this habitat, as opposed to other vegetated biotopes (Schenker & Block 1986). The similarities in the fellfield habitats and on Marion Island also extend to the species level. For example, the collembolan *Cryptopygus antarcticus* (of which the sub-species *C. antarcticus travei* (Déharveng) is endemic to Marion Island) and cryptostigmatid mite, *Magellozetes antarcticus* (Michael) (known to display a preference for unvegetated areas, Tilbrook 1967), both widely distributed in Antarctic fellfields (Pugh 1993; Convey 1994), seem to be found only in fellfield areas on Marion Island (Gabriel 1999). Furthermore, *A. selago* cushions in the Marion Island fellfield, and moss-turves on maritime Antarctic islands seem to provide a remarkably similar habitat to arthropods in these regions. These two unrelated vegetation types are very similar structurally, with dense growth forms and small interstices that can only be exploited effectively by the smaller species for refugia (West 1982). The mites, *Eupodes minutus* and *Ereynetes macquariensis* Fain and collembolan, *C. antarcticus* exist at very similar high densities in these habitats (Goddard 1979; Usher & Booth 1986).

The fellfield vegetation complex is further characterised by few alien species (only three insect species and a single springtail are thought to be introduced) compared with other vegetation types on Marion Island, where alien insects and Collembola may contribute as much as 50% of the species richness, and may predominate in terms of numbers and contribution to ecosystem functioning (Hänel & Chown 1999; Gabriel 1999). The generally low abundance and high species richness of arthropods in the fellfield on Marion Island may explain the small proportion of the total arthropod species richness accounted for by alien species in this vegetation complex. The harsh physical environment (implied by low densities especially during winter, see also Schenker & Block 1986) in this vegetation complex could make initial establishment of propagules more difficult, while high species richness might make invasion more difficult as a consequence of some form of biotic resistance (see Davies 1987; Brown 1995; Chown *et al.* 1998; Brandjes *et al.* 1999 for further discussion). On the other hand, distance from the likely source of introductions (see Gremmen & Smith 1999 for a review of plant introductions and the role of the scientific station) seems less likely an explanation because most alien species are widespread in the lowland vegetation complexes (Hänel *et al.* 1998; A.G.A. Gabriel, unpublished data).

Although the epilithic biotope and *Azorella*-cushions shared most species, there were major differences between these habitat components in the abundance and dominance of these species (Table 2.2). The highest mean annual abundance for a species in *A. selago* cushions (*ca.* 16000 individuals.m^{-2} for *E. minutus*) was an order of magnitude greater than that of the most abundant species in the epilithic biotope (*ca.* 700 individuals.m^{-2} for *H. fulvus*), and arthropods generally displayed much higher densities in the former, even for the same species (an exception is *H. fulvus* that showed a similar density in both components). In the cushions, Collembola and

Prostigmata were the more common groups, while the Cryptostigmata were commonest in the epilithic biotope. Insect abundance was very low, with the notable exceptions of the introduced thrip, *Apterothrips apteris*, in the *A. selago* cushions and the endemic cryptogam-feeding weevil, *Bothrometopus elongatus* in the epilithic biotope (Barendse & Chown in press).

These differences may have been due to the different sampling methods (and hence areas sampled) used for the two components, and this may have resulted in an under-representation of certain taxa, especially the more cryptic and fragile prostigmatid mites which may have been damaged or destroyed in the sampling process (see Block 1984; Gaston *et al.* 1999; Van Rensburg *et al.* in press). Despite this, we are of the opinion that most taxa were sampled efficiently, and that our technique represented the most appropriate compromise between habitat-associated sampling requirements and equivalence of sample unit area. Therefore, the differences between species abundance and dominance in the two habitat components may be attributable to their different structural and physical features. Although *A. selago* cushions occupy a relatively small surface area (<10%) in the fellfield habitat, they represent the dominant vascular plants, and a stable, relatively warm and homogenous habitat with a concentration of resources, compared to rocky areas (Huntley 1971, 1972; Chown & Crafford 1992). Arthropods in the epilithic biotope are probably subjected to more environmental extremes such as temporary flooding, freeze-thaw cycles, and disturbance of the substrate by wind and water (Chown 1993a; Chown *et al.* 1997; Blake 1996). Thus it seems likely that the *A. selago* cushions represent resource islands within the otherwise more hostile fellfield. This conjecture deserves further attention, especially given the role of this species in community succession on Marion Island, and elsewhere in the sub-Antarctic (Scott 1985; Frenot *et al.* 1997).

In a multivariate comparison of the acarine communities, and in the presence of an additional vascular plant habitat (*Poa cookii* tussock grassland), the above differences in arthropod community structure between the two fellfield habitat components do not emerge clearly when species qualitative data are used. Here, analysis based on presence/absence data only clustered the two fellfield habitats together, when compared with the species rich mite community from lowland *Poa cookii* tussock grassland. However, when the quantitative data were used, the two vascular communities clustered together while excluding the epilithic habitat component at the 50% similarity level (Fig. 2.2). This is largely because the shared mite species have similar densities in the two vascular plant habitats, in contrast to their densities in the epilithic habitat component. Thus a faunistic survey might have concluded that, in terms of its arthropod community, the fellfield habitat could be considered a single unit, whereas this is clearly not the case. Rather, it should be viewed as a complex of two habitat components with rather different arthropod communities occurring in each component, but with potential species exchange and interactions (see also below).

This simple example has several, broader, implications. Insects and other arthropods have been recognised as potentially important biological indicators (see McGeoch 1998) for example in the selection of suitable conservation areas (Usher & Edwards 1986) or to demonstrate the effects of environmental change (such as climatic change and habitat alteration; see De Groot *et al.* 1995; Davies & Melbourne 1999). However, it would be unwise to gauge changes in an environment, or their effects on a biota, solely on the presence or absence of taxa (such as is suggested by Davies & Melbourne 1999). Such data may give little indication of more subtle changes in community structure (and thus ecosystem function) generally expected with changes in habitat quality or climate (Karieva *et al.* 1993; Van Rensburg *et al.* 1999), and because abundances change within and between these different habitat components at different times (i.e. there are phenological differences, see below). The chironomid midge, *Limnophyes minimus*, introduced to Marion Island, further serves to illustrate this point. Although its presence in all vegetated habitats on the island was well documented (Crafford *et al.* 1986), its high abundance and substantial contribution to nutrient cycling only became apparent with quantitative sampling (Hänel & Chown 1998).

Seasonality

Based on our data two major seasonal patterns in abundance emerged: summer peaks and an aseasonal pattern. We acknowledge that limited inferences can be made about exact phenologies by examining fluctuations in abundance alone, and that some of these patterns may have been due, for example, to movement of species between habitat components, or seasonal movements deeper into the substrate (e.g. Usher & Booth 1984). Although data from two or more seasons (e.g. West 1982) and from a variety of life stages (see Booth & Usher 1986; Bellido *et al.* 1988) would be necessary for more conclusive interpretation of seasonality, we are of the opinion that our data are sufficient for an initial interpretation of such patterns in the fellfield, and that observed fluctuations are the result of reproductive cycles in the majority of cases (see also Barendse & Chown in press). The variety of seasonal responses found in the fellfield arthropods is not unusual, and has indeed been found for arthropods elsewhere (Niijima 1975; Hutson & Veitch 1983; Badejo 1990; Badejo & Van Straalen 1993; Stamou *et al.* 1993). However, it has been suggested that in sub-Antarctic species distinct seasonal patterns are generally uncommon (Convey 1996a, 1996b, 1997a, 1997b). Rather, flexibility of responses, and an aseasonal pattern are thought to be more likely because the sub-Antarctic is a region characterised by relatively weak seasonal cues due to its limited temperature variation (see Fig. 2.5 and Schulze 1971). Our data suggest that while the former, aseasonal pattern may be common in some species, in line with especially Convey's (1996a) suggestions, programmed responses to some seasonal cue may be as, or more common. Danks (1999) recently suggested that while many polar species exhibit flexibility, a programmed response might still occur in certain critical stages in their life cycles. In the absence of data on prominent seasonal cues (see

Wolda 1988; Tauber & Tauber 1991; Tauber *et al.* 1998), and on life histories, we suspect that this latter, programmed response is common to many of the fellfield arthropods, especially because seasonal responses vary greatly between the two fellfield habitat components. These habitat components differ considerably in their microclimates (see above; Huntley 1971; Chown & Crafford 1990; Blake 1996), which may have a large effect on the phenology of the species occurring in them, especially those with low vagility (see Hodkinson *et al.* 1998 for similar observations for the High Arctic). In addition, it seems unlikely that the broad range of taxa occurring in this habitat complex should necessarily exhibit similar seasonality patterns when even closely related taxa can show widely different patterns, both in the sub-Antarctic (Davies 1972; West 1982; Chown & Scholtz 1989; Chown 1993b) and elsewhere (e.g. Leinaas & Fjellberg 1985).

Our data on the seasonality of higher taxonomic groups, as opposed to that of single species, clearly illustrates the pitfalls of drawing conclusions based on such combined data, a practice regularly applied in soil arthropod ecology (e.g. Hijii 1987; Hutson & Veitch 1987; Hijii 1989; Al-Assiuty *et al.* 1993; Butterfield 1999; see also Basset 1991; Novotny & Basset 1998 for examples from other habitats). In general, the seasonality pattern of the numerically dominant species tends to obscure those shown by less dominant species (Figs 2.4A - C). Thus, conclusions based on higher taxa are likely to be erroneous in those cases where the higher taxa are represented by more than a single species, or in those cases where distinct, but different patterns are present in two or more abundant species. This could lead to an apparent aseasonal or multi-peaked pattern. Using genera as a collective unit is unlikely to constitute a significant problem in this regard because the frequency distribution of the numbers of species within genera is more uniform than the frequency distribution of species numbers per higher taxon above this level (Dial & Marzluff 1989). However, grouping species by hierarchical levels from family upwards for studies of seasonality of the soil biota is likely to deliver results of dubious validity and should be discontinued, difficult as this might be (see also Osler & Beattie 1999).

In conclusion, we have shown that there are distinct differences in the arthropod communities inhabiting the two major habitat components of the fellfield vegetation complex on Marion Island, both in terms of their seasonality and abundance. However, these differences would have been obscured had our study focussed on higher taxa or simply constituted a faunal survey, and would undoubtedly have led to erroneous conclusions regarding these communities. Given that significant climate change is taking place on sub-Antarctic islands (Allison & Keage 1986; Smith & Steenkamp 1990; Frenot *et al.* 1997), and that differential changes in the seasonality and abundance of alien (as opposed to indigenous species) are thought to be the most likely biotic responses to these changes (Smith & Steenkamp 1990; Chown & Smith 1993; Chown 1997; Arnold & Convey 1998; Morewood & Ring 1998), our conclusions show that quantitative surveys of the fauna at the species level are essential for detecting and monitoring this change. This is true also of more direct habitat change, and is a conclusion not unique to studies in the sub-Antarctic (e.g. De Groot *et al.* 1995). Hence, in our view, our study constitutes further strong motivation for quantitative work in soil biology, echoing the earlier plea of Usher *et al.* (1982).

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Chapter 3. Habitat specificity of mites on Marion Island

> "Where are your combing seas, your blue water, your rollers,
> your breakers, your whales, or your waterspouts, and your endless motion,
> in this bit of a forest, child?"
>
> **James Fenimore Cooper - The Pathfinder**

Introduction

Because of their location just to the south or north of the Antarctic Polar Frontal Zone (APFZ), the sub-Antarctic islands of the southern ocean have cold climates that are neither as extreme as those of the Antarctic, nor as mild as those of more temperate regions. In consequence, these islands support a range of vegetation types that vary considerably with altitude. Higher altitude areas tend to be dominated by typically Antarctic fellfield, or wind desert areas, while the lowlands have a closed, tundra-like vegetation (Gremmen 1981; Bergstrom & Chown 1999). On the basis of their histories, the fellfield habitats and the rocky shoreline areas characteristic of most of these islands (e.g. de Villiers 1976; Knox 1994), have been grouped together as the epilithic biotope, by Chown (1989). The habitats constituting this epilithic biotope are thought to have been continually present during the glacial cycles that affected most of these islands (see Hall 1990; Chown 1994; Bergstrom & Chown 1999), although their ranges may have expanded and contracted with climatic fluctuations. On the other hand, the vegetation types characterised by vascular plants (i.e. those constituting the vegetated biotope) are thought to have been largely absent at the height of the Neocene glaciations, but more extensive during interglacial periods, with the exception perhaps of a few species such as those in the genera *Lyallia* and *Azorella* which may have been present at the glacial maxima (Schalke & Van Zinderen Bakker 1971; Young & Schofield 1973; Scott 1985).

Investigations of the insect faunas of the sub-Antarctic islands have suggested that differences in habitat specificity and the extent of interspecific interactions in these two major biotopes may be a consequence of the substantial differences in their age, and extent of disturbance. Thus, insects in the vegetated biotope show little habitat specificity (Chown 1989; Chown & Scholtz 1989; Crafford 1990), although their may be habitat-associated differences in dominance and abundance (Vogel 1985). Likewise interspecific interactions in this biotope are rare or non-existent, and this is thought to be largely a consequence of low species richness, low niche occupancy, and abundant resources (Crafford *et al.* 1986; Crafford 1990). Such a paucity of interspecific interactions is in keeping with what theory would predict for an apparently stable, though adverse environment, where resource constraints should be more important than biotic interactions (Southwood 1977; Greenslade 1983; Holm 1988).

In contrast, habitat specificity in the epilithic biotope is reasonably common. Coastal habitats such as rocky shores and boulder beaches possess many, habitat specific insect species

(Crafford *et al.* 1986; Crafford & Scholtz 1987; Chown 1990), and this appears to be true also of fellfield (Davies 1973; Chown 1989, 1990). In epilithic habitats biotic interactions are also more common than in the vegetated biotope. For instance, parasitism is common on the shore (see Crafford *et al.* 1986), while interspecific competition is thought to be present both here and in fellfield (e.g. Davies 1972, 1987; Chown 1992). These findings seem to conform to theoretical predictions. For example, both Connell (1975, 1980) and Menge & Sutherland (1987) suggested that competition is most likely in moderately harsh physical environments, while Arthur (1987) argued that older communities are more likely to be structured by interspecific interactions than younger ones. Likewise, Holm (1988) suggested that given sufficient time, and hence the accumulation of species, interspecific interactions are likely to develop in stable, adverse environments.

Nonetheless, these generalisations concerning community structure in sub-Antarctic arthropods are not universally supported. For example, Vogel (1985) suggested that the favourable conditions found in lowland vegetated habitats, as opposed to the harsher conditions in the epilithic habitats (e.g. osmotic stress, greater exposure, and more pronounced environmental extremes, see de Villiers 1976; Chown & Crafford 1992; Blake 1996), might encourage habitat specificity.

Despite the fact that the arthropod faunas of the sub-Antarctic islands are now relatively well known (Pugh 1993; Greenslade 1990; Crafford *et al.* 1986; Marshall *et al.* 1999; Chown *et al.* 1998), there have been few quantitative studies of micro-arthropod communities (see West 1982, 1984; Bellido & Cancela Da Fonseca. 1988 for exceptions). Furthermore, none of these have set out to provide an independent test of the hypothesis that there are biotope-related differences in habitat specificity on the sub-Antarctic islands, despite the opportunity such a test provides for examining the broad applicability of the ideas concerning arthropod community structure in the sub-Antarctic espoused by previous authors (see above).

Therefore, the aim of this study is to provide just such a test using the Acari, an arthropod order that is not only more speciose in the sub-Antarctic than is the Insecta (compare Crafford *et al.* 1986 and Marshall *et al.* 1999), but which has also evolved independently of the latter group. This is accomplished by an examination of mite community patterns and habitat specificity across 17 different habitats, belonging to both the epilithic and vegetated biotopes, on sub-Antarctic Marion Island.

Material and Methods

Study area

The South African possessions of Marion (46° 54'S, 37°45'E) and Prince Edward Islands (see Fig. 3.1) are typically sub-Antarctic in terms of their location, climate, geology and biology (see Van Zinderen Bakker *et al.* 1971; Smith 1987; Hänel & Chown 1999 for general information on climate, geology, biota and human presence on the islands).

This study considered habitats both from the vegetated (vascular vegetation) and epilithic biotopes (a rocky shore and mid-altitude fellfield) (see Tables 3.1-3.3). The selection of the vegetated habitats was based on Gremmen's (1981) six community-complexes (containing 41 phytosociologically based plant communities) that were grouped according to species composition and in some cases, structural and ecological factors. For the purposes of this study, representative examples of plant communities within each of these complexes, occurring at and below altitudes 400 metres above sea-level (a.s.l.), were chosen (Hänel 1999).

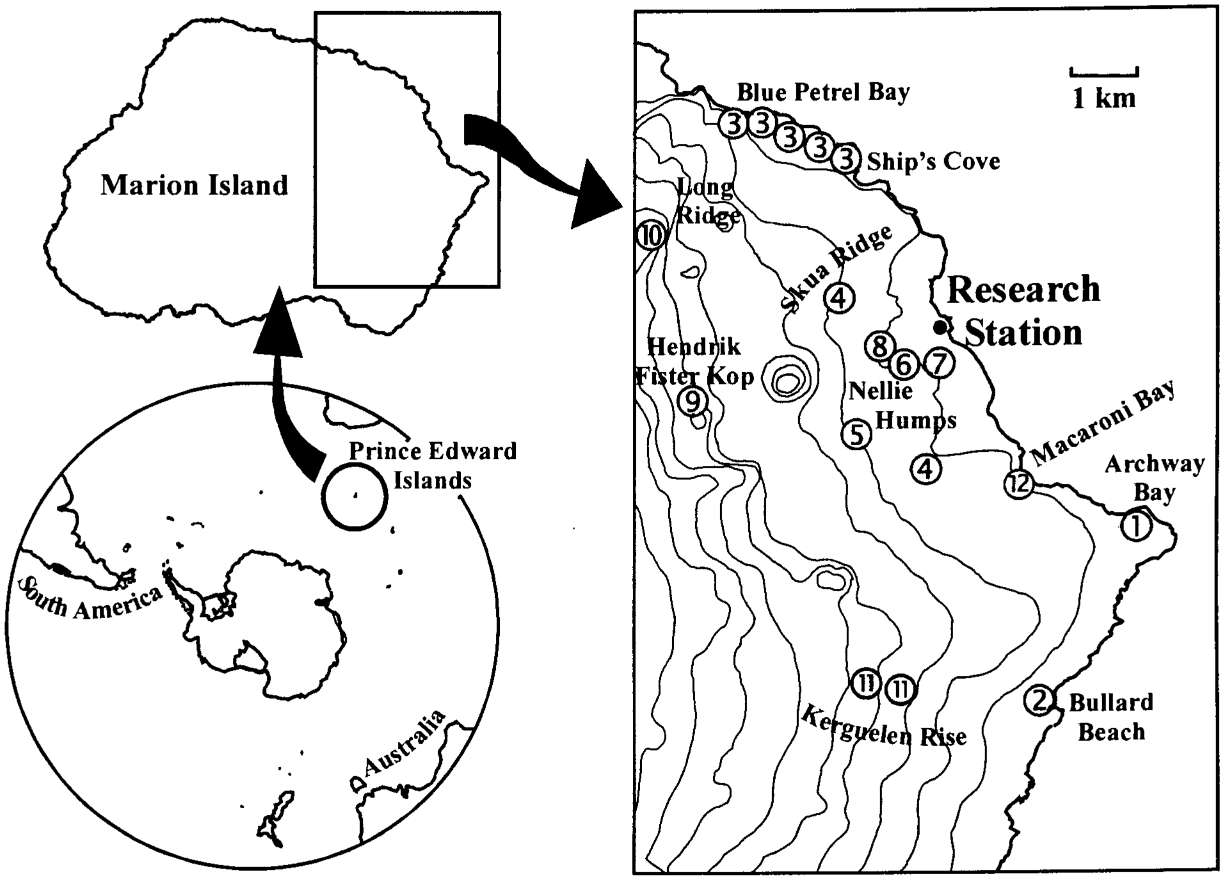

Figure 3.1 Locality map showing position of the Prince Edward Islands in the South Polar region, an outline of Marion Island, with the east coast enlarged to indicate the positions of sampling sites. Contours at 50m intervals. **Communities:** 1 = *Crassula moschata* herbfield; 2 = *Poa cookii* tussock grassland; 3 = *Cotula plumosa* herbfield; 4 = *Acaena magellanica* drainage line; 5 = *Blechnum penna-marina* lowland slope; 6 = *Blepharidophyllum densifolium* mire; 7 = *Sanionia uncinatus* mire; 8 = *Jamesoniella colorata* mire; 9 = Mid-altitude mire; 10 = High-altitude mire; 11 = Mid-altitude fellfield (which includes both *Azorella selago* cushions and epilithic biotope); 12 = Rocky shore.

Table 3.1 Description of the two habitat components in the exposed, grey-lava, mid-altitude fellfield (after the fjaeldmark habitat complex of Gremmen 1981) on Kerguelen rise (300m a.s.l.), Marion Island (see Fig. 3.1).

Azorella selago cushions	**Epilithic component**
Distinct cushions of various shapes and sizes dispersed throughout the fellfield and covering less than 10% of the total surface area. Grasses, clubmosses and ferns sometimes grow epiphytically on the cushions.	A mixture of boulders, rocks and gravel, which may be sorted by wind or freezing. Numerous encrusting, and cushion- and ball-forming bryophytes. Also contains organic material derived from *A. selago* and abundant cryptogams.

Table 3.2 Selected representative plant communities in the vegetated biotope on the east coast of Marion Island (Adapted from Gremmen 1981, Smith 1987 and Hänel 1999) (see Fig. 3.1).

Plant community-complex (after Gremmen 1981)	**Representative plant communities**	**Description**	**Location and approximate altitude**
Salt-spray (*Crassula moschata*) complex	*C. moschata* halophylic herbfield	Dense mats of the succulent herb, found in shore-zone areas affected by wind-blown sea spray	Coastal cliffs at Archway Bay (20m a.s.l.)
Biotically influenced (*Callitriche antarctica – Poa cookii*) complex	*P. cookii* tussock grassland	Dense stands of tussocks, found in areas influenced by trampling and manuring of animals, in this case penguins	Adjacent macaroni penguin colony, Bullard Beach North (20m a.s.l.)
	Cotula plumosa herbfield	Lush stands of the feathery leafed herb, found in shallow manured soils, also associated with salt-spray	Coastal stretch between Blue Petrel Bay and Ship's Cove (20m a.s.l.)
Drainage line (*Acaena magellanica – Brachythecium*) complex	*A. magellanica* drainage line	Tangled mats growing in areas with pronounced subsurface water movement, such as river banks, in springs, flushes, water tracks and drainage lines	Two inland sites, one at Tom, Dick and Harry (75m a.s.l.), and the other at Skua Ridge (100m a.s.l.)
Fernbrake (*Blechnum penna-marina*) complex	*B. penna-marina* lowland slope	Well-drained, relatively dry lowland slopes, dominated by *B. penna-marina*	Nellie Humps (100m a.s.l.)
Oligotrophic (*Juncus scheuchzerioides – Blepharidophylum densifolium*) mire complex	*Blepharidophyllum densifolium* mire *Sanionia uncinatus* mire *Jamesoniella colorata* mire	Areas of peat accumulation with impeded drainage. These three species of bryophytes are important peat-forming plants	All sites in the area between the Scientific Station and Nellie Humps (50m a.s.l.)
	Mid-altitude mire		Near Hendrik Fister Kop (250m a.s.l.)
	High-altitude mire		Long Ridge South (400m a.s.l.)

Table 3.3 Description of the littoral and supralittoral zones on the rocky shore habitat at Macaroni Bay on the east coast of Marion Island (after de Villiers 1976; Mercer *et al.* in prep.).

Littoral zones	**Supralittoral zones**
Red algal zone: Above the upper limit of bull kelp *Durvillaea antarctica*. Submerged during high tide. Completely covered by filamentous, foliose and encrusting Rhodaphyta.	*Mastodia* zone: Dominated by the dark foliose thalli of the genus *Mastodia*.
Porphyra zone: The mid-littoral zone dominated by the rhodaphyte genus *Porphyra*.	*Caloplaca* zone: The uppermost supralittoral zone covered by a bright yellow encrusting lichen from the genus *Calloplaca*.
Verrucaria zone: First lichen dominated zone which marks the upper littoral. Almost continuously encrusted by the dark grey to black encrusting lichen. Falls in the splash zone.	

All sampling sites were on the eastern side of the island within a radius of about five kilometres from the research station (Fig. 3.1). One of these complexes, fellfield (also called wind-desert or fjaeldmark), dominates in terms of surface area of the island at and above 300m a.s.l., except for a small area (*ca.* 10 km^2) of permanent ice-cap (Verwoerd 1971). This complex forms in areas strongly exposed to wind, on a variety of different substrata (scoria and grey lava) and with varying degrees of vegetational cover. The dicot, *Azorella selago* Hook f. is conspicuously present as discrete cushions in fellfields of up to 750 m a.s.l., above which cryptogams dominate (Huntley 1972; Gremmen 1981). Therefore, the fellfield complex cannot strictly be termed a vegetation type because it contains both vegetated and epilithic components. For this study, the *A. selago* cushions within the fellfield habitat studied here were considered part of the vegetation complexes in the vegetated biotope (after Gremmen 1981), while the rocky debris in-between cushions belonged to the epilithic biotope (see Chown 1989). Throughout this paper, the fellfield habitat/complex will refer to this habitat as a whole, including both the epilithic and vegetated components (see Table 3.1). The individual components are referred to specifically where applicable.

The vegetated habitats (= complexes), excluding the *A. selago* cushions, can be broadly divided into non-mire and mire communities. Five representatives of each were chosen and each of these two groups, in turn, contained subdivisions (Table 3.2). The division between the different types of oligotrophic mires is somewhat arbitrary because they all belong to the *Juncus scheuchzerioides – Blepharidophylum densifolium* community-complex and only differ in dominant bryophyte species. The mid-and high-altitude mires are both high altitude variants of *Jamesoniella grandiflora* dominated mires (Gremmen personal communication).

The other epilithic biotope considered was a gently sloping, unbroken rocky shore. Five distinct zones were distinguished based on distance from the high water mark and the type of algal or lichen cover present (de Villiers 1976; Mercer *et al.* in prep.). These zones could further be divided into three littoral and two supralittoral zones (see Table 3.3).

Sampling protocol

The sampling programme spanned two years (June 1996 to April 1998). All habitats from the vegetated biotope, with the exception of *A. selago* cushions, were sampled during the first year (1996/97). Non-mire communities (see Table 3.3) were sampled from June 1996 and every alternate month thereafter up to May 1997, while mire communities were similarly sampled from July 1996 onwards up to June 1997. The fellfield (which includes *A. selago* cushions and the epilithic biotope) and rocky shore habitats were sampled during the second year (1997/1998). The shore was sampled from June 1997 and every second month thereafter, up to April 1998. Fellfield was sampled every alternate month from July 1997 to April 1998 (the last month sampled for both shore and fellfield was April 1998 due to logistic constraints).

In the case of all vegetated habitats, excepting *A. selago* cushions and the high-altitude mire, five 2 x 2 m quadrats were arbitrarily placed in homogenous patches considered representative of each vegetation type. Due to the small available area of the high-altitude mire, only four 1 m^2 quadrats were chosen in this community. The distances between quadrats within a vegetation type varied from a minimum of 20 m in the *Blechnum penna-marina* fernbrake to a maximum of about 3.5 km in the case of *Cotula plumosa* herbfield (see Fig. 3.1).

In the fellfield habitat the two habitat components (*A. selago* cushions and epilithic biotope) were considered separately because they required different sampling approaches, and to avoid trampling resulting from sampling both components in a single transect. Two replicate transects (80 x 40 m) were chosen, each consisting of two adjoining, identical sub-transects (80 x 20 m) made up of four 20 x 20 m quadrats. One sub-transect was used for sampling of the epilithic component and the other for *A. selago* cushions.

All vegetated habitats were sampled by coring using an O'Connor split-corer (Southwood 1978; Edwards 1991) (inside diameter of core = 70 mm and height = 70 mm; surface area ≈ 0.0039 m^2). Five cores were collected at randomly determined positions (or cushions for *A. selago*) from each quadrat. Thus, 25 cores per sampling month were taken from habitat types with five quadrats (a total of 150 samples for the year, except for *Cotula plumosa* where 25 samples were subsequently lost (i.e. n = 125). Twenty cores per month were taken from communities with four quadrats (high-altitude mire and *A. selago* cushions), thus a total of 120 samples were taken from the high-altitude mire, and 240 *A. selago* cushions were sampled (120 in each of the two replicates). Micro-arthropods were extracted from cores with modified Macfadyen high gradient extraction (extraction protocol: two days at 25 °C followed by two days at 30 °C, Macfadyen 1961). Specimens were retained in 95% ethanol until further examination.

The fellfield epilithic biotope was sampled by randomly collecting five 30 x 30 cm sampling grids from each of the four quadrats per month (i.e. 20 samples per transect per month and a total of 240 samples for both transects for the year). A sample consisted of the upper layer of loose rock and plant (i.e. grass, mosses, detritus) material scraped from within a 30 x 30 cm sampling grid down to no deeper than 10 cm. Sampling was biased in that *A. selago* cushions and large boulders were purposely avoided, because the former were sampled separately and the latter could not be sampled using this sampling method. Arthropods were first extracted on-site by means of flotation in sieved (125 μm mesh-size) cold water from a nearby perennial stream. Samples were washed three times each, sieved through 125 μm mesh, and stored in plastic jars for transport back to the laboratory where further extraction of arthropods from samples was achieved by means of differential wetting (Southwood 1978) with kerosene and 70% ethanol (aqueous phase).

The rocky shore was sampled by establishing six transects (a different one was randomly selected for each sampling month) perpendicular to the shoreline and stretching from the lower littoral to upper supralittoral. All samples were collected on a single day near the date of spring low tide. Ten samples were randomly selected from a sampling grid (1x1 m) consisting of 100 smaller squares (0.1 m^2) within each of the five zones along the transect (thus a total of 60 samples per zone for the entire period). Samples were collected by scraping lichen/algae down to the bare rock from within a circular plastic tube into a plastic vial, using a scalpel blade. Due to the variable nature of the lichen and algal cover of the different zones, tubes of two different diameters were used (inside diameter of tube = 70 mm for Red, *Porphyra* and *Mastodia* zones and 35 mm for *Verrucaria* and *Caloplaca*). Samples were retained in 70% ethanol.

Finally, for all collected samples, arthropods were separated by hand under a binocular dissecting microscope. Insects and Collembola were considered in separate studies (Chapter 2; Gabriel 1999; Hänel 1999; Barendse & Chown in press; Mercer *et al.* in prep.). Mites were sorted into species or morphospecies, identified to the lowest possible taxonomic level and counted (Krantz 1978; Marshall *et al.* 1999; D.J. Marshall personal communication). All life stages within species were combined. Samples are housed at the Universities of Durban-Westville and Pretoria.

Data analyses

Raw counts for species were converted to densities per m^2 for all samples. Mean annual abundance (± standard error) in each habitat was calculated per species, and for all species combined.

Abundance data were subjected to multivariate analysis using the program PRIMER v4.0 (Clarke & Warwick 1994). Densities obtained for replicate samples within each quadrat and across all months were summed to avoid the effects of seasonality and to accommodate a large data set (see Clarke 1993). This resulted in five replicates for each vegetated habitat, except for the high-altitude mire, which had four. The two fellfield habitats, *A. selago* cushions and epilithic biotope, had eight replicates each and the rocky shore zones 10 each. A cluster analysis using group-average clustering and based on Bray-Curtis similarity measures was carried out to compare the different predetermined habitats in terms of acarine abundance (see Fig. 3.2). Data were double square-root transformed prior to analysis in order to weight common and rare species equally (see Clarke & Warwick 1994). Due to the great dissimilarity between some of the habitats and the associated scale problems, these data were not represented as an ordination plot. The similarities between the more closely clustered terrestrial habitats (thus excluding the shoreline habitats) were further represented as a non-metric multi-dimensional scaling (MDS) ordination plot. Analysis of similarity (ANOSIM) was used to test for significant differences between all the habitat types (see Clark 1993). This is a non-parametric permutation procedure applied to the rank similarity matrix underlying sample ordinations that calculates a global *R*-statistic. If *R* falls between the values zero and one it indicates some degree of discrimination between habitat types, the closer to one the higher the significance (Clarke & Warwick 1994).

Furthermore, using the same species-abundance matrix, the extent of habitat specificity that each species or taxon of mite displays for each habitat type was determined using the Indicator Value Method (IndVal) described by Dufrêne & Legendre (1997). This procedure expresses the degree of specificity (uniqueness to a habitat) and fidelity (frequency of occurrence throughout a habitat) as a percentage. A high percentage IndVal indicates both high habitat specificity and fidelity for a species and suggests that a species is highly representative of the habitat in question. Thus, a species with a high IndVal is not only unique to a habitat but has a high probability of being present in any sample from that habitat (see McGeoch & Chown 1998). For this study species that reached their maximum and significant ($P < 0.05$) IndVal for a specific habitat were taken to be strong indicator species for that habitat. No level of significance can be calculated for species achieving maximum IndVals at the first level (i.e. for all habitats), because of the random reallocation procedure of habitats among habitat groups used to calculate the Indvals (Dufrêne & Legendre 1997). These species represent extreme habitat generalists.

Results

Mites were identified to the lowest possible taxon, 39 in total from 27 families (Table 3.4). Marshall *et al.* (1999) provided a revised catalogue of the mites of Marion Island which lists 60 free-living acarine species and sub-species. Considering the large number of new records and undescribed species (Marshall *et al.* 1999), coupled with the scale of the study and the limitations of a dissecting microscope in identifying smaller cryptic groups (such as the Prostigmata), identification down to species level was not possible in some cases. Therefore, in many cases the family name used in the analysis refers to more than one species.

Table 3.4 Complete list of Acarine taxa identified in 17 habitats (vegetated and epilithic) on Marion Island, and used in analyses (after Marshall *et al.* 1999). Feeding biologies: P=predatory; A=algal feeder; F=fungal feeder; L=lichen feeder; D=detritivore (?? = most likely, but not certain).(Sources: 1 = Strong 1967; 2 = Fitzsimons 1971; 3 = Gressitt & Shoup 1967; 4 = Goddard 1982; 5 = Behan-Pelletier & Hill 1983; 6 = Norton 1985).

Order	**Family**	**Species**	**Feeding biology**
Mesostigmata	Rhodacaridae	Gen.? spp. ?	P
	Digamasellidae	*Dendrolaelaps* sp. ?	P
	Cillibidae	Gen.? sp. ?	F??
	Ologamasidae	Gen.? sp. ?	P
Prostigmata	Nanorchestidae	*Nanorchestes* spp. ?	A[2, 3, 4]
	Eupodidae	*Eupodes minutus* (Strandtmann)	A/F[2, 4]
	Rhagidiidae	*Rhagidia* sp. ?	P[1]
	Ereynetidae	*Ereynetes macquariensis* Fain	A/F[4]
	Tydeidae	*Tydeus* /*Pertydeus* spp.?	A/F/L[1,2, 4]
	Unknown prostigmatid sp.	*Tydeus* sp. ?	A/F/L[1,2, 4]
	Bdellidae	*Bdellodes* sp. ?	P
	Stigmaeidae	*Eryngiopus* sp. 1 (fellfield)	L??
		Eryngiopus sp. 2 (shoreline)	L??
	Erythraeidae	*Balaustium* sp. ?	P
	Tarsonemidae	Gen.? sp. ?	F[6]
	Pygmephoridae	Gen.? sp. ?	F[6]
	Halacaridae	*Halacarellus* sp. ?	??
		Isobactrus magnus (Lohmann)	??
Cryptostigmata	Brachythonidae	*Liochthonius australis* Covarrubias	D/A/F/L??[5]
	Peloppiidae	*Macquarioppia striata* (Wallwork)	D/A/F/L??[5]
	Oppiidae	*Austroppia crozetensis* (Richters)	F/D[1]
	Ameronothridae	*Halozetes fulvus* Engelbrecht	L/D[1, 4]
		Halozetes belgicae (Michael)	D/A/F/L??[5]
		H. marinus devilliersi Engelbrecht	D/A/F/L??[5]
		H. marionensis Engelbrecht	D/A/F/L??[5]
		Podacarus auberti Grandjean	D/A/F/L??[5]
		Alaskozetes antarcticus (Michael)	D/A/F/L??[5]
	Oribatulidae	*Dometorina marionensis* van Pletzen & Kok	D/A/F/L??[5]
	Ceratozetidae	*Magellozetes antarcticus* (Michael)	A/D[1]
	Parakalummidae	*Porokalumma rotunda* Wallwork	??
Astigmata	Acaridae	*Schwiebea talpa subantarctica* Fain	F??
	Algophagidae	*Algophagus* sp. 1 (vegetated biotopes)	A/F??
		Algophagus sp. 2 (fellfield)	A/F??
		Algophagus sp. 3 (shoreline)	A/F??
	Winterscmidtiidae	*Neocalvolia* sp. 1	F??
		Neocalvolia sp. 2	F??
		Neocalvolia sp. 3 (shoreline)	F??
	Hyadesiidae	*Hyadesia halophila* Fain	A??
		H. kerguelensis Lohmann	A??

In certain cases where there could be accurately distinguished between unidentified members from the same family, especially from different habitats, these were kept separate. Accordingly, the following should be noted (Marshall *et al.* 1999; Marshall unpublished data). Rhodacaridae may refer to up to five different species of which some may be habitat specific. Cillibidae refers to a single unknown species, a first record for the sub-Antarctic. Nanorchestidae may include four species some of which are possibly habitat specific. The family Rhagidiidae includes a single unknown species. Tydeidae includes all tydeid mites, possibly representing more than one species or genus (*Tydeus* or *Pertydeus*). The unknown prostigmatid mite found only in *Crassula moschata* and *Poa cookii* (Table 3.5) is also thought to be a species of *Tydeus*, but was distinct enough not to warrant its inclusion in the Tydeidae group. The *Eryngiopus* spp. represents a new sub-Antarctic record. The specimens found in the fellfield and on the shore were kept separate (*Eryngiopus* sp.1 and 2). The Algophagidae is a peculiar group with possibly as many as five species. For these analyses three distinct species were distinguished, one from vegetated biotopes (*Algophagus* sp. 1), one from the fellfield complex (*Algophagus* sp. 2), and another from the shoreline (*Algophagus* sp. 3). The family Winterschmitiidae contains three putative species belonging to the genus *Neocalvolia* (spp. 1, 2 and 3), the first two being found in some vegetated habitats and the latter on the shoreline. *Hyadesia kerguelensis* and *Hyadesia subantarctica* were both present, but were combined under the former species. The species *Isobactrus magnus* may contain specimens of *Rhombognathus auster*, if this species were present. Three additional species that were not recorded in Marshall *et al.* (1999) were present in the sampled. These are individuals from the mesostigmatid family Ologamasidae, commonly found in, and apparently restricted to the vegetated biotopes, and two small unidentified species of prostigmatid mites from the families Tarsonemidae and Pygmephoridae.

The likely feeding biology of each species/taxon is included in Table 3.4. Some of these have been experimentally determined (Gressitt & Shoup 1967; Strong 1967; Fitzsimons 1971; Goddard 1982), although others are based on more general works (e.g. Krantz 1978; Norton 1985), and may be inaccurate as far as food preference or specificity for particular species is concerned. Cryptostigmata especially, can have a wide range of feeding strategies (Behan-Pellitier & Hill 1983; Norton 1985; Maraun *et al.* 1998).

Prostigmata were the most speciose group with 14 species/taxa, followed by Cryptostigmata (12), Astigmata (9), and Mesostigmata (4) (Table 3.4). In terrestrial habitats (Table 5) Cryptostigmata and Prostigmata were the numerically dominant groups with densities of the latter reaching >18 000 individuals.m^{-2}. The Astigmata reached a higher abundance within the shoreline habitats (Table 3.6) than in any of the terrestrial habitats, with *Hyadesia halophila* in the *Mastodia* zone reaching the highest densities of any species in any habitat (>80 000 individuals.m^{-2}). Both Cryptostigmata and Prostigmata were also highly abundant in the shoreline habitats. Cryptostigmata generally showed the highest abundance throughout all habitat types (ranging from *c.*780 to *c.* 130 000 individuals.m^{-2}) followed by the Prostigmata. Mesostigmata were more abundant in terrestrial habitats than on the shoreline. Taxa known to be predatory (Table 3.4) were generally less abundant than fungivores and detritivores, though predatory Rhodacaridae and Ologamasidae (Mesostigmata) reached high densities in some habitats (Table 3.5).

The shoreline habitats, except for the *Caloplaca* lichen zone, (Table 3.7) displayed higher mite densities than any of the terrestrial habitats. *Azorella selago* cushions displayed the highest densities for vegetated habitats with the very high density of *Eupodes minutus* (Prostigmata) in this habitat making the greatest contribution. Among the terrestrial habitats, non-mire vegetation types consistently showed higher abundances than either mire habitats or the fellfield epilithic biotope. In terms of species/taxon richness (Table 3.7) the shoreline habitats housed fewer species (ranging from 6-13) than the terrestrial habitats (ranging between 17 and 22). The mire habitats had slightly fewer species than the non-mire and fellfield epilithic habitats.

The dendrogram of the cluster analysis (Fig. 3.2) clearly shows a separation, firstly, between the littoral and other habitats, and secondly, between the supralittoral and strictly terrestrial habitats (at *c.* 10% similarity). Furthermore, the various shore zones separate discretely, except for the two lowermost Red and *Porphyra* zones. Next, the fellfield epilithic biotope is separated from the vegetated biotope. The non-metric MDS ordination on abundance for terrestrial habitats (Fig. 3.3) shows this clear separation between the epilithic and vegetated biotope, and a further separation between mire and non-mire vegetation types. Analysis of similarity (ANOSIM) indicated significant differences (Global $R = 0.941$; $P < 0.01$) between all *a priori* defined habitat types (Table 3.6). For all pairwise comparisons of habitats $P < 0.024$.

Table 3.5 Annual mean densities per m² (mean ± standard error) of Acari in 12 different terrestrial habitats (fellfield and vegetated) on Marion Island. (Acaena = *Acaena magelanica*; Blech = *Blechnum penna-marina*; Cot = *Cotula plumosa*; Crass = *Crassula moschata*; Poa = *Poa cookii*; Bleph = *Blepharidophylum densifolium*; San = *Sanionia uncinatus*; Jam = *Jamesoniella colorata*; Hi = High-altitude mire; Mid = Mid-altitude mire; Azorella = *Azorella selago*; Epilith = epilithic biotope in mid-altitude fellfield). ** indicates density of less than one specimen per m². *n*=150 for all except Hi (*n*=120), Cot (*n*=125), Azorella and Epilith (*n*=240 for both).

Order/species	**Acaena**	**Blech**	**Cot**	**Crass**	**Poa**	**Bleph**	**San**	**Jam**	**Hi**	**Mid**	**Azorella**	**Epilith**
Mesostigmata (all)	**3101±527**	**1912±226**	**7683±815**	**2796±322**	**2668±276**	**953±193**	**1682±360**	**702±135**	**323±56**	**597±125**	**1657±100**	**149±11**
Rhodacaridae	591± 84	338±40	1825±152	1647±122	1266±131	184±32	133±42	71±13	21±7	95±20	723±61	24±4
Dendrolaelaps sp.	62 ± 23	62±28	293±95	102±40	69±16	19±14	10±5	16±5	3±2	5±3	281±23	7±1
Cillibidae	1770±446	1495±197	2330±454	303±53	826±131	726±187	1523±353	612±131	227±45	473±120	652±69	117±10
Ologamasidae	677±125	17±7	3235±394	743±220	506±95	24±9	16±5	3±2	7±3	5±3	-	-
Prostigmata (all)	**3558±273**	**2224±152**	**3033±479**	**4424±344**	**1391±170**	**1123±145**	**298±41**	**1176±144**	**253±49**	**407±54**	**18294±869**	**43±4**
Nanorchestes spp.	10±5	196±40	-	4±4	-	4±2	-	-	-	42±28	662±106	1±0
Eupodes minutus	1046±168	700±103	2039±416	1346±224	542±103	447±131	130±33	400±67	92±36	177±36	15828±790	2±0
Rhagidia sp.	-	-	-	-	-	-	-	-	-	-	23±6	1±0
Ereynetes macquariensis	263±76	30±12	23±11	107±23	85±22	40±11	26±10	29±10	2±2	12±6	1183±80	1±0
Tydeidae	1983±233	1026±127	518±75	2562±260	579±88	579±78	64±12	627±111	104±19	104±19	538±63	16±3
Bdellodes sp.	220±31	64±11	17±8	64±53	49±15	16±6	28±8	80±15	2±2	16±6	28±6	13±1
Eryngiopus sp. 1	-	-	-	-	-	-	-	-	-	-	4±2	7±1
Balaustium sp.	-	28±11	-	-	83±39	-	-	-	-	-	-	**
Tarsonemidae	10±9	-	17±8	4±2	17±6	-	-	5±5	-	-	-	-
Pygmephoridae	24±11	2±2	64±29	241±133	14±6	38±17	50±15	35±9	2±2	57±16	31±8	2±1
Unidentified prostigmatid	-	-	-	97±33	23±19	-	-	-	-	-	-	-
Cryptostigmata (all)	**986±177**	**3099±322**	**5211±462**	**7950±680**	**5749±419**	**3984±408**	**3534±333**	**4944±442**	**788±90**	**2120±228**	**5451±433**	**1215±58**
Liochthonius australis	2±2	2±2	-	83±57	-	210±113	-	-	2±2	35±28	25±6	11±3
Macquarioppia striata	12±5	113±20	607±137	930±289	1632±227	64±20	2±2	326±158	130±44	13±2	258±44	13±2
Magellozetes antarcticus	-	-	-	-	-	-	-	-	-	-	2±2	24±8
Halozetes fulvus	102±21	511±92	1960±265	4802±479	2600±245	929±164	1479±208	317±51	140±22	442±56	683±70	725±48
Podacarus auberti	61±20	99±43	1318±160	393±57	1109±99	258±196	95±17	35±11	33±9	50±12	18±10	**
Dometorina marionensis	269±81	669±81	119±37	1429±182	139±36	2048±293	1323±147	3726±340	300±40	1221±190	402±52	239±25
Austroppia crozetensis	540±144	1713±241	1208±203	930±289	270±93	476±88	634±157	540±142	31±9	81±36	4063±391	202±25
Astigmata (all)	**109±73**	**31±10**	**489±96**	**81±31**	**73±22**	**47±12**	**130±30**	**29±10**	**22±7**	**31±9**	**41±8**	**7±2**
Schwiebea talpa	94±73	2±2	127±28	5±3	4±2	42±12	111±29	29±10	10±4	26±8	37±7	**
Algophagus sp. 1	-	14±8	21±13	7±3	21±12	3±2	16±8	-	7±3	3±2	-	-
Algophagus sp. 2	-	-	-	-	-	-	-	-	-	-	1±1	7±2
Neocalvolia sp. 1	5±3	10±5	129±33	43±21	14±6	-	-	-	-	-	-	-
Neocalvolia sp. 2	10±6	5±4	212±63	26±11	35±14	2±2	3±2	-	-	2±2	-	-

Table 3.6 Annual mean densities (± S.E., individuals.m^{-2}, n=60) of the mites for the five different littoral and supralittoral zones on the rocky shore at Macaroni Bay, Marion Island (adapted from Mercer *et al.* in prep.).

Species/taxon	**Red zone**	***Porphyra* zone**	***Verrucaria* zone**	***Mastodia* zone**	***Caloplaca* zone**
Astigmata					
Algophagus sp. 3	-	-	-	219 ± 81	-
Hyadesia halophila	-	-	-	211724 ± 31743	2984 ± 1381
H. kerguelensis	23001 ± 4099	36684 ± 4138	85228 ± 10390	-	-
Neocalvolia sp. 3	-	-	-	11 ± 8	1340 ± 523
Cryptostigmata					
Alaskozetes antarcticus	-	-	-	4059 ± 1346	-
Halozetes belgicae	6 ± 4	26 ± 16	265 ± 124	130380 ± 25393	1817 ± 779
H.marinus devilliersi	44 ± 14	8 ± 5	27 ± 27	8 ± 5	0
H. marionensis	570 ± 139	396 ± 84	6698 ± 1009	3841 ± 1244	0
Podacarus auberti	-	8 ± 5	-	12748 ± 3608	27 ± 19
Porokalumma rotunda	-	-	-	8 ± 5	1777 ± 701
Mesostigmata					
Dendrolaelaps sp.	-	-	-	42 ± 21	199 ± 52
Rhodacaridae	-	-	27 ± 19	415 ± 80	-
Prostigmata					
Eupodes minutus	-	-	-	-	66 ± 34
Halacarellus sp.	12 ± 8	11 ± 11	-	-	-
Isobactrus magnus	3804 ± 795	3705 ± 975	23608 ± 5766	87 ± 25	-
Eryngiopus sp. 2	-	-	-	351 ± 94	2281 ± 412
Tydeidae	3 ± 3	-	-	-	703 ± 148

Table 3.7 Annual mean mite density ± standard error (individuals.m^{-2}) per sample and species richness in 17 different habitats. For all terrestrial habitats n=150 except high-altitude mire (n=120), *Cotula plumosa* (n=125), *Azorella selago* and epilithic biotope (n=240 each). n=60 for all shore-line zones.

"Group"	Habitat	Annual mean density ± S.E. (individuals.m^{-2}) per sample for all species	Species richness
Rock shore	Red algal zone	27439±4510	7
	Porphyra algal zone	40838±4235	7
	Verrucaria lichen zone	115852±14975	6
	Mastodia lichen zone	363890±37200	13
	Caloplaca lichen zone	11194±2439	9
Non-mires	*Cotula plumosa* herbfield	16416±1166	19
	Crassula moschata herbfield	15251±953	22
	Poa cookii tussock grassland	9881±610	21
	Acaena magelanica	7754±804	20
	Blechnum penna-marina	7274±536	21
Mires	*Jamesoniella colorata* mire	6851±586	16
	Blepharidophylum densifolium mire	6106±515	19
	Sanionia uncinatus mire	5644±601	17
	Mid-altitude mire	3137±323	19
	High-altitude mire	1112±119	17
Fellfield	Epilithic biotope in fellfield	1414±65	21
	Azorella selago cushions	25443±1131	20

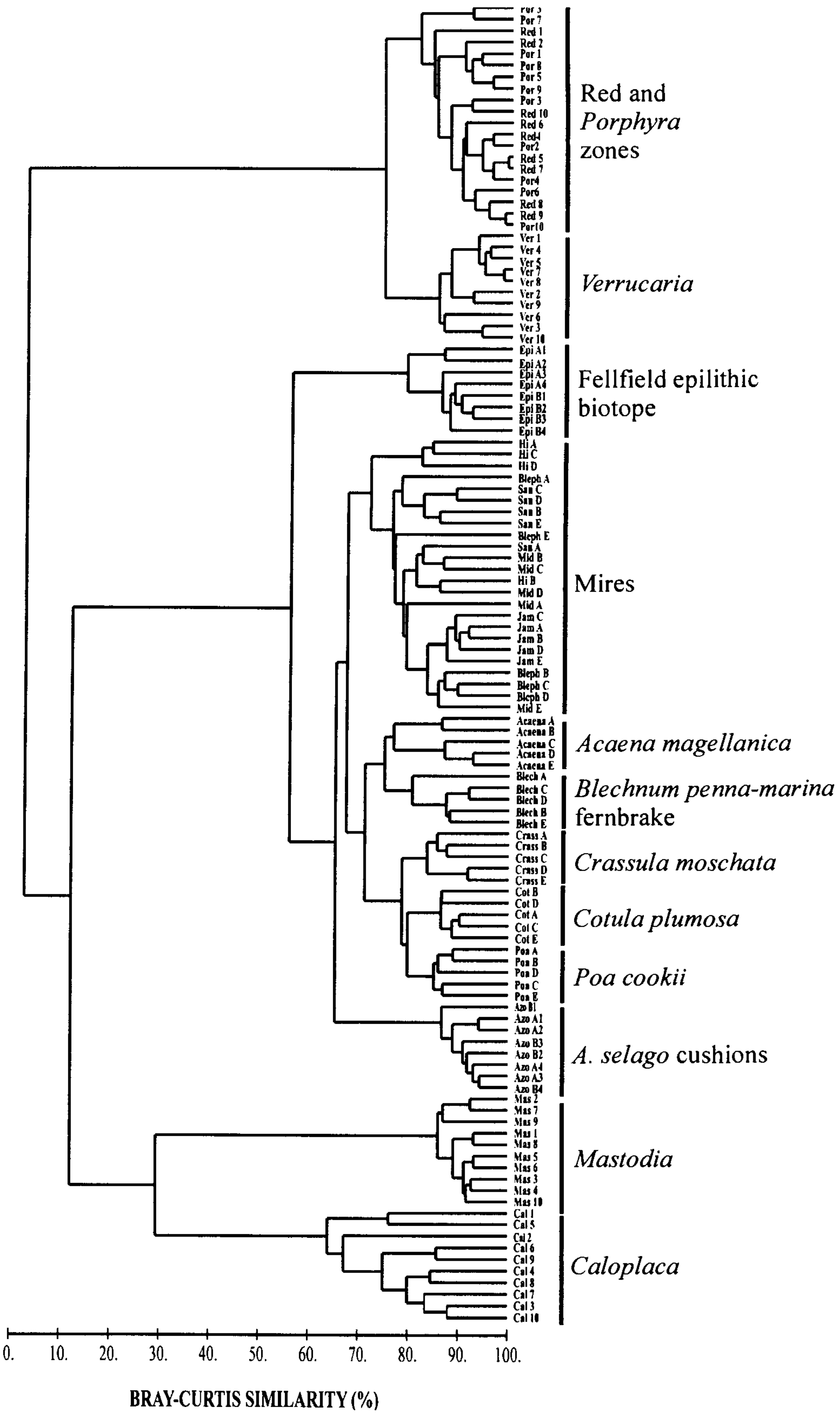

Figure 3.2 Dendrogram of cluster analysis of mite abundances in 17 habitats (vegetated and epilithic) on Marion Island.

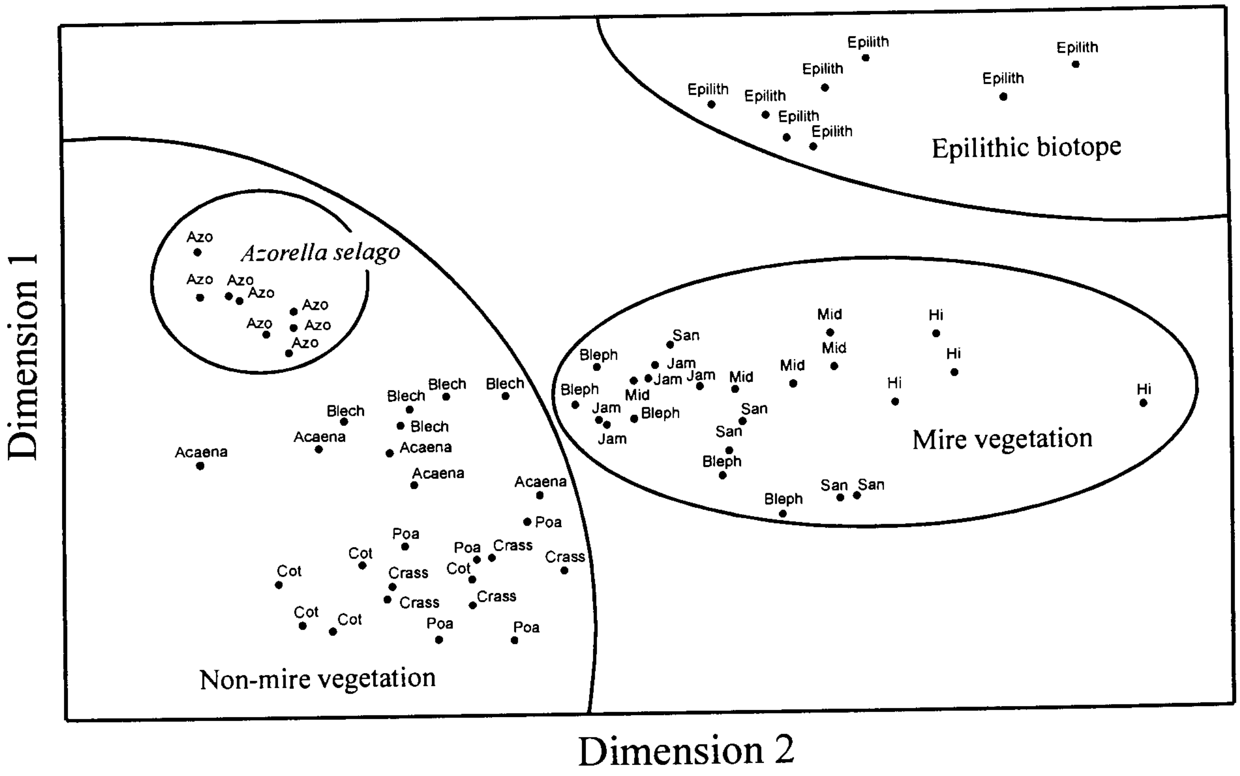

Figure 3.3 Non-metric MDS ordination of abundances of mite species in 12 terrestrial habitats (fellfield and vegetation) (stress = 0.13). Acaena = *Acaena magelanica*; Blech = *Blechnum penna-marina*; Cot = *Cotula plumosa*; Crass = *Crassula moschata*; Poa = *Poa cookii*; Bleph = *Blepharidophylum densifolium*; San = *Sanionia uncinatus*; Jam = *Jamesoniella colorata*; Hi = High-altitude mire; Mid = Mid-altitude mire; Azo = *Azorella selago*; Epilith = epilithic biotope in mid-altitude fellfield.

No taxa reached their maximum indicator values at the first level of all habitats (see Fig. 3.4). At the second level, the three littoral habitats (Fig. 3.4, Box A), as a group, had four characteristic species which could be considered generalists within these zones, while the Red/*Porphyra* zone combination had the single (though non-significant) *Halacarellus* sp. as indicator. The two supralittoral habitats (Fig. 3.4, Box B), as a group, had two characteristic species, while the *Mastodia* and *Caloplaca* zones had four and two indicator species respectively. Ten species/taxa reached their maximum IndVals at the level of all terrestrial habitats and are thus generalists in these habitats. Both fellfield habitat components, i.e. *Azorella selago* cushions and the epilithic component (Fig. 3.4, Box C), had three specific species each. All vegetated habitats as a group had two characteristic species. Of the habitats from the vegetated biotope, only the salt-spray and biotically influenced group had species specific to these habitats (Fig. 3.4, Box D). No species were characteristic of individual mire habitats, nor to mires as a group.

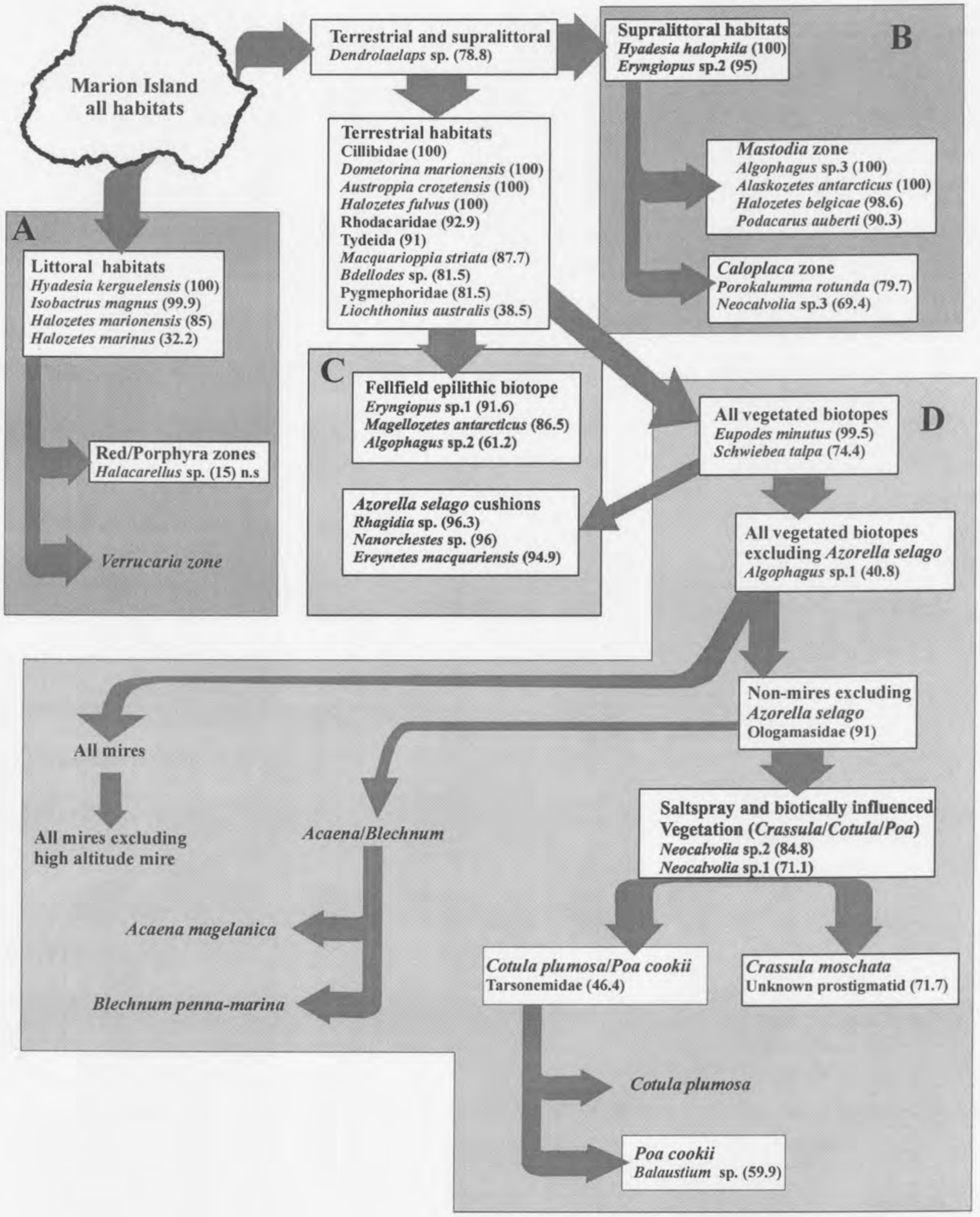

Figure 3.4 Flow diagram showing indicator species reaching their maximum indicator values in the habitat groups distinguished by the cluster analysis (Fig. 2) (IndVals in brackets, all significant at $P < 0.05$ except where indicated by n.s.). Boxes: **A** = Littoral habitats; **B** = Supralittoral habitats; **C** = Fellfield habitats; **D** = All closed lowland vegetated habitats (excluding *Azorella selago*).

Discussion

The annual mean abundances (Table 3.7) recorded in some of the habitats resemble those found in habitats on other sub-Antarctic islands. The exceptionally high acarine densities found in the littoral zones are comparable to those found on Kerguelen Island (Bellido 1981; Mercer *et al.* in prep.), while the higher abundances in *Azorella selago* cushions and halophylic herbfields approximate those found in South Georgian grasslands and mossbanks (see West 1984). The mites in the remainder of the terrestrial habitats have lower densities. This trend of higher mite densities in vascular vegetation compared with bryophyte-dominated mires, is in keeping with the patterns displayed by indigenous Collembola (Gabriel 1999) and insects (Hänel 1999) on Marion Island, and is probably a consequence of differences in plant standing crop between these habitats (Gabriel 1999; see also Smith 1976, 1988).

Despite high densities in the rocky shore habitats, species richness was considerably lower here than in the terrestrial habitats (Table 3.7). The species richness of terrestrial habitats did not differ greatly, though non-mire habitats had slightly more species than mires. Most species occurred in all or most of these habitats and only a small proportion of species were restricted to single habitats or habitat groups. Four species were unique to the two fellfield habitat components (Table 3.5), and these were also amongst the indicator species for these habitats (see below). The only other terrestrial habitats that included species with a restricted occurrence were the salt-spray and biotically influenced vegetation types.

The cluster analysis indicated that the rocky shore habitats have a distinct assemblage composition and structure, different from that of the terrestrial habitats, although the supralittoral does share some species with some vegetated habitats. However, these species are likely to be transient species (tourists, see Mercer *et al.* in prep.) that are not true resident members of, in this case, the rocky shore. Therefore, the classification of epilithic biotope habitats (shore and fellfield) on the basis of glacial and geological history is not entirely reflected by their mite communities because they share no species and have distinct community structures. Although most mite species occur in all vegetation types, it seems that differences in the vegetation types are reflected by community structure (in terms of dominance and abundance), and that groups of similar or related vegetation types host more similar communities (e.g. salt-spray and biotically influenced habitats). Mire communities were more closely related to each other than to other vascular plant types. However, the distinction between different mire communities are less clear-cut that those between different vascular plants, probably because they are all variants of the *Juncus scheuchzerioides–Blepharidophylum densifolium* community-complex (Gremmen 1981).

Of particular interest is that the *Azorella selago* cushions exhibited greater similarity to other lowland vascular plant habitats in terms of mite community structure than they did to the epilithic component of the fellfield complex. These cushions, though sharing all except one species with the epilithic component, can therefore be viewed as discrete habitat islands belonging to the vegetated biotope (see Chapter 2), and may represent an ecotonal habitat between lowland vegetation and high altitude fellfield habitats. This is especially significant in the light of the past and present position of *A. selago* in the vegetation of Marion Island. *Azorella selago* exhibits the highest standing crop of any vascular plant on Marion Island (Huntley 1972) and is an important component in most vegetation complexes (Smith 1976; Gremmen 1981). It is also important in the initial stages of vegetational succession, e.g. in peat formation (Frenot *et al.* 1998). Palynological evidence from Marion Island and elsewhere (see Schalke & Van Zinderen Bakker 1971; Young & Schofield 1973; Scott 1985) suggests that a fellfield-like habitat dominated by *Azorella*-cushions existed throughout glaciation and these cushions, which can be of considerable individual age (Huntley 1972; Frenot, *et al.* 1993), probably represent the oldest vascular plant habitat on Marion Island. Their much higher mite densities compared to the epilithic component also suggests that these cushions are very stable, homogenous habitats with a concentration of resources, compared to the rocky areas. This is supported by favourable microclimatic measurements of temperature within cushions, shown to be consistently three or four degrees higher than ambient air temperatures (Crafford 1990), the storage of heat energy from radiation for considerable periods after sunset (Huntley 1971), and the cushion growth form that is thought to be highly resistant to frost and wind damage (Huntley 1972). All these features would make *A. selago* cushions exceptionally suitable glacial refugia. It has been hypothesised (Chown 1989, 1990) that during the height of the glaciations, arthropods retreated to unglaciated epilithic havens from where they subsequently re-colonised newly established vegetated habitats, at the termination of glaciation. The distinctness of the shoreline fauna and the few species shared with terrestrial habitats suggest that the coastal habitats played a limited role as glacial retreats. An examination of indicator species further supports this notion (Fig. 3.4). Almost all species in the rocky shore habitats are restricted to these areas (Fig. 3.4, Boxes A and B), while the terrestrial habitats share most species and many habitat generalists occur there. Only a few species, such as *Halozetes fulvus* and *Neocalvolia* spp. (this genus seems restricted to the shore and adjacent salt-spray vegetation) seem likely colonists from the shoreline into the vegetation (see Mercer *et al.* in prep.). On the other hand, judging from the species distribution overlap and preponderance of generalists in the vegetated habitats, it seems that recolonisation from a fellfield habitat, and especially the *A. selago* component, is a more feasible explanation. This is supported by the fact that the *A. selago* cushions currently house more similar mite communities (in terms of density) to other vegetated biotopes, than to the fellfield epilithic biotope. In addition, *A. selago* is still an important component, or is at least present, in most other vegetation complexes (Gremmen 1981). Furthermore, the highly specific indicator species for the two fellfield habitats (Fig. 2.4, Box C) either have limited distribution in other habitats, or are completely absent. Interestingly, some of these habitat specific species show strong biogeographical affinities to the harsher maritime and continental Antarctic habitats, e.g. *Magellozetes antarcticus* which is known to show preference for rocky, unvegetated habitats elsewhere in the Antarctic (Tilbrook 1967; Pugh 1993; Convey 1994) and *Rhagidia sp., Nanorchestes spp. and Ereynetes macquariensis* (all indicator species for *A. selago* cushions) that are common inhabitants of maritime Antarctic moss turves, which seem to share many structural similarities with these cushions (Goddard 1979; West 1982; Usher & Booth 1986). Species such as *M. antarcticus* and *Rhagidia* sp. could be relicts from when fellfields represented the most favourable and only habitable areas during glaciation.

In sum, the analysis of mite communities suggests that the generalist strategy is common in terrestrial habitats, especially for Cryptostigmata, which probably have flexible feeding strategies, and predatory taxa, predation being the oldest and most general feeding strategy in arachnids (see Norton 1985; Maraun *et al.* 1998). Mites within the epilithic biotope (i.e. those in fellfield and shoreline habitats) displayed a higher incidence of habitat specificity than those in the vegetated biotope, and the rather different glacial histories of these two biotopes seems a likely explanation for this. The large number of species shared by all terrestrial vegetated habitats could be due to the recolonisation of all current habitats from the same glacial refugium, most likely *A. selago* cushions in a fellfield habitat. It is possible that greater taxonomic resolution within some of the more poorly known groups (such as the Rhodacaridae) would reveal further habitat specific species. Further investigations into abundance covariance and inter-and intraspecific interactions would also be useful in determining whether similar, consistent differences between the habitats occur in terms of interspecific interactions within the Acari. Nonetheless, there does seem to be some support for the notion that habitat specificity is more well developed in the epilithic than in the vegetated biotope, thus substantiating earlier hypotheses based on insect distributions.

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Chapter 4. The biology of *Bothrometopus elongatus* (Coleoptera, Curculionidae) in a mid-altitude fellfield on sub-Antarctic Marion Island[**]

> "On one side hung a very large oil painting so thoroughly besmoked, and every way defaced, that in the unequal crosslights by which you viewed it, it was only by diligent study and a series of systematic visits to it, and careful inquiry of the neighbors, that you could any way arrive at an understanding of its purpose. Such unaccountable masses of shades and shadows, that at first you almost thought some ambitious young artist, in the time of the New England hags, had endeavored to delineate chaos bewitched. But by dint of much and earnest contemplation, and oft repeated ponderings, and especially by throwing open the little window towards the back of the entry, you at last come to the conclusion that such an idea, however wild, might not be altogether unwarranted. But what most puzzled and confounded you was a long, limber, portentous, black mass of something hovering in the centre of the picture over three blue, dim, perpendicular lines floating in a nameless yeast. A boggy, soggy, squitchy picture truly, enough to drive a nervous man distracted. Yet was there a sort of indefinite, half-attained, unimaginable sublimity about it that fairly froze you to it, till you involuntarily took an oath with yourself to find out what that marvellous painting meant. Ever and anon a bright, but, alas, deceptive idea would dart you through.- It's the Black Sea in a midnight gale.- It's the unnatural combat of the four primal elements.- It's a blasted heath.- It's a Hyperborean winter scene.- It's the breaking-up of the icebound stream of Time. But last all these fancies yielded to that one portentous something in the picture's midst. That once found out, and all the rest were plain. But stop; does it not bear a faint resemblance to a gigantic fish? even the great leviathan himself?"
>
> **Herman Mellville – Moby Dick**

Introduction

The *Ectemnorhinus*-group (Coleoptera: Curculionidae) is one of the most speciose, monophyletic taxa found on the islands of the Southern Ocean. Consequently, these weevils contribute considerably to species richness on the South Indian Ocean Province (SIP) Islands (*sensu* Lewis Smith 1984) to which they are restricted (Chown 1994; Kuschel & Chown 1995). Thus it is unsurprising that considerable information is available on the habitat use, diet, and physiology of many of the species within the *Ectemnorhinus*-group (e.g., Dreux 1972; Dreux & Voisin 1986; Davies 1973; Chown 1992, 1993a, 1994; Chown *et al.* 1997; Van der Merwe *et al.* 1997). However, the life histories of few of the species are known.

Of the 36 species constituting the *Ectemnorhinus*-group, the biology and ecology of only two have been investigated in any detail. Chown & Scholtz (1989a) and Chown (1990) provided detailed information on the life history strategies and biology of two closely related *Ectemnorhinus* species, *E. similis* C.O. Waterhouse and *E. marioni* Jeannel, found in lowland areas on Marion Island. However, Chown (1989, 1994) noted that on most SIP islands the majority of the species within the *Ectemnorhinus*-group of genera do not occur in this lowland,

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vegetated biotope. Indeed only some members of the genus *Ectemnorhinus*, and three species within the genera *Christensenia* and *Canonopsis*, are routinely found in this biotope and, curiously, only a subset of these feed on angiosperms (Chown 1994). The remainder of the genera in the group, that is, *Disker* (1 sp.), *Palirhoeus* (1 sp.) and *Bothrometopus* (17 spp.) and the species in *Ectemnorhinus* (*Xanium*) (4 spp.) occur in the epilithic biotope (shoreline rocks, coastal and inland rock faces, and fellfield) and feed exclusively on cryptogams (Chown 1989; Chown 1994).

Despite the preponderance of *Ectemnorhinus*-group species in the epilithic biotope, little is known concerning their biology. Chown (1993b) used measurements of the head capsules of larvae of *Palirhoeus eatoni* (C.O. Waterhouse) and *Bothrometopus randi* Jeannel from Marion Island to suggest that these species both have seven larval instars, that they have overlapping generations in the field, and that seasonal peaks in their abundance are probably not marked. Although his sampling was conducted over only two months, in April/May 1992, Chown's (1993b) study is the only one on the biology of epilithic weevil species undertaken to date (see Convey 1996a; Hänel & Chown 1999a). Here we address this lacuna by providing information, collected over a full year, on the life history of *Bothrometopus elongatus* (Jeannel), a species common in fellfield on Marion Island (Chown 1989).

Material and methods

Bothrometopus elongatus is endemic to the sub-Antarctic Prince Edward Islands (Marion, 46°54'S 37°45'E, and Prince Edward, 46°38'S 37°57'E) (Kuschel & Chown 1995), and the fieldwork for this investigation was undertaken on Marion Island, the site of the South African scientific station (see Van Zinderen Bakker *et al.* 1971; Smith 1987; Hänel & Chown 1999b for general information on the climate, geology, biota, and history of human occupation of this island).

Adults and larvae of *B. elongatus* were collected during a quantitative ecological programme that examined arthropod communities in all the major terrestrial habitats on Marion Island. The study site from which this species was collected (GPS location: 46°55'17.8"S, 37°51'28.7"E, elevation: 250 m above sea level), was situated on Kerguelen Rise, a typical, mid-altitude, grey lava fellfield area on the south-eastern side of Marion Island. Fellfield (also known as wind-desert or fjaeldmark) is one of six major vegetation community-complexes recognised on the Prince Edward Islands (Gremmen 1981). Fellfield forms in rocky areas strongly exposed to wind and is characterised by a low percentage of plant cover, dominance by bryophytes, and reduced temperatures compared with lower lying areas (Gremmen 1981). A conspicuous component of mid-altitude fellfield is the cushion-forming dicot, *Azorella selago* Hook. f. (Apiaceae) (Huntley 1972; Gremmen 1981).

Two transects, each 80 m long and consisting of four 20 x 20 m quadrats were selected. Sampling was conducted bimonthly between July 1997 and April 1998, with the exception of concurrent March/April samples at the end of the study (due to logistical time constraints). Where possible, days with favourable weather conditions (no wind and rain) were selected for sampling. Five samples were collected at random from each quadrat during each sampling interval. This gives 20 samples per transect per interval, and a grand total of 240 samples for both transects for the entire study period.

Each sample consisted of the upper layer of loose rock and plant material collected from within a 30 cm x 30 cm sampling grid down to no deeper than 10 cm. Sampling was biased in the sense that *A. selago* cushions and large boulders were purposely avoided. *A. selago* cushions were sampled separately, but rarely contained *B. elongatus* (see Chown 1989) and thus these data are not considered here. Boulders could not be sampled due to their large size. The material obtained from each sample was placed in a plastic bucket from which arthropods were extracted on-site by flotation in cold water (sieved through 125 μm nylon mesh) obtained from a perennial stream located nearby. Samples were washed three times and the supernatant from each wash poured through a 125 μm mesh. The material collected in the sieve was stored in individual plastic jars and returned to the laboratory within six hours for further extraction. Further laboratory extraction was done using differential wetting (Southwood 1978), with 70% alcohol and kerosene. Specimens were stored in 95% ethanol.

Adult and larval weevils were hand separated from the other arthropods, and identified to species under a dissecting microscope (keys provided by Crafford *et al.* 1986 and Chown & Scholtz 1989b). The number of adults and larvae per sample was converted to density (individuals per m^2) and bimonthly mean (± S.E.) densities were calculated. Differences between months were tested for significance using Kruskal-Wallis analysis of variance (ANOVA) by ranks (samples were not normally distributed) and Dunn's multiple comparison test (Zar 1996).

Head capsule widths of larvae were measured using an ocular micrometer on a dissection microscope. Following Chown & Scholtz (1989a) and Chown (1993b) (see also Logan *et al.* 1998 and references therein) a histogram of head capsule widths was then used to determine the number of instars present in this species. Size limits to each instar were determined from the measurement histogram, and these were subsequently used to determine the number of larvae in each instar.

Additional data on the number and size of developing eggs within females at any given time, together with information on feeding habits of the adults and larvae from this and other sites on Marion Island, were collected by SLC in the period 1986-1999 (see Chown 1989; Chown & Scholtz 1989c; Chown 1992; Chown 1993b; Chown 1994 for additional information on sites and collection techniques).

Results

The frequency histogram of head capsule widths indicates that *B. elongatus* larvae has six, or possibly seven, larval instars (Fig. 4.1). Very low numbers, both in total and on a bimonthly basis, excluded the seventh instar as valid, and the size range of the sixth instar was increased to include the few, larger individuals (Table 4.1).

Instar I and II larvae were dominant in July, September and November (Fig. 4.2). First instar density reached its maximum in November, indicating substantial egg-laying activity and subsequent eclosion in early summer. Instar II larvae reached their numerical peak in January, while third instar larvae were most abundant in November, January and March, reaching a peak in the latter month together with instar IV. Both instars V and VI reached maximum densities in April, but at much lower densities than the earlier instars, suggesting an increase in larval mortality at the end of summer, and from instars II and III onwards.

Age-related, or seasonal larval mortality, is apparent in the larval density estimates (Fig. 4.3) with larval density declining significantly from a November peak. Adult density also showed significant seasonal changes, with a density peak in September (Fig. 4.4). On collection, female *B. elongatus* contained 3.13 ± 0.27 eggs (mean ± S.E., n = 30, range: 1 - 6) with a length of 0.61 ± 0.011 mm (mean ± S.E., n = 26, range: 0.47 - 0.75).

Table 4.1 Instar head capsule widths (mm) for *Bothrometopus elongatus* collected from 1997 to 1998 at Kerguelen Rise on Marion Island.

Instar	*n*	Mean ± S.E.	Range
I	403	0.1891 ± 0.0003	0.1667 – 0.1905
II	615	0.2312 ± 0.0005	0.2024 – 0.2400
III	390	0.2766 ± 0.0006	0.2500 – 0.2933
IV	305	0.3203 ± 0.0007	0.2976 – 0.3333
V	201	0.3633 ± 0.0007	0.3529 – 0.3810
VI	82	0.4220 ± 0.0023	0.3929 – 0.4762

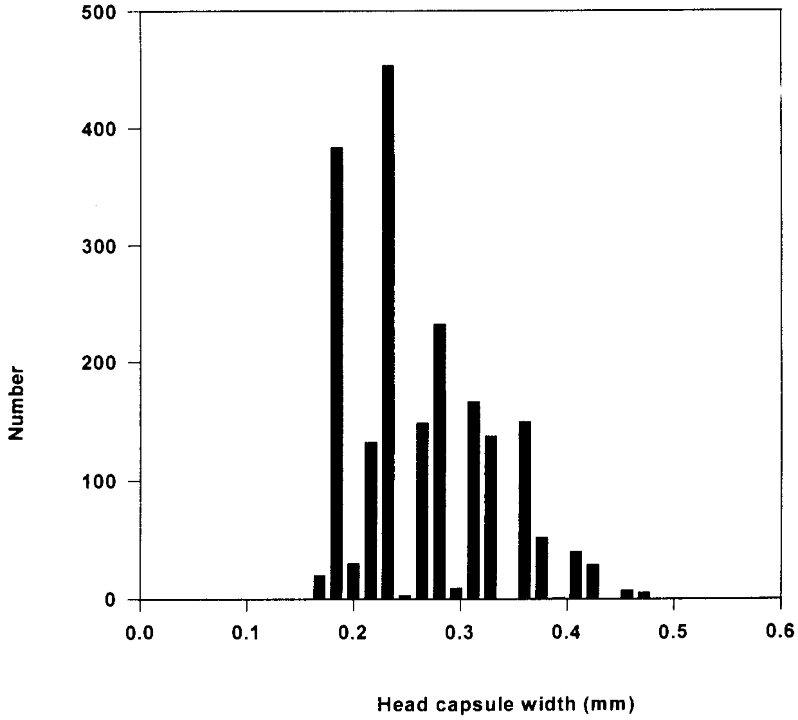

Figure 4.1 Frequency histogram of head capsule widths (mm) of *Bothrometopus elongatus* (Jeannel) larvae collected at Kerguelen Rise, Marion Island (n = 1996).

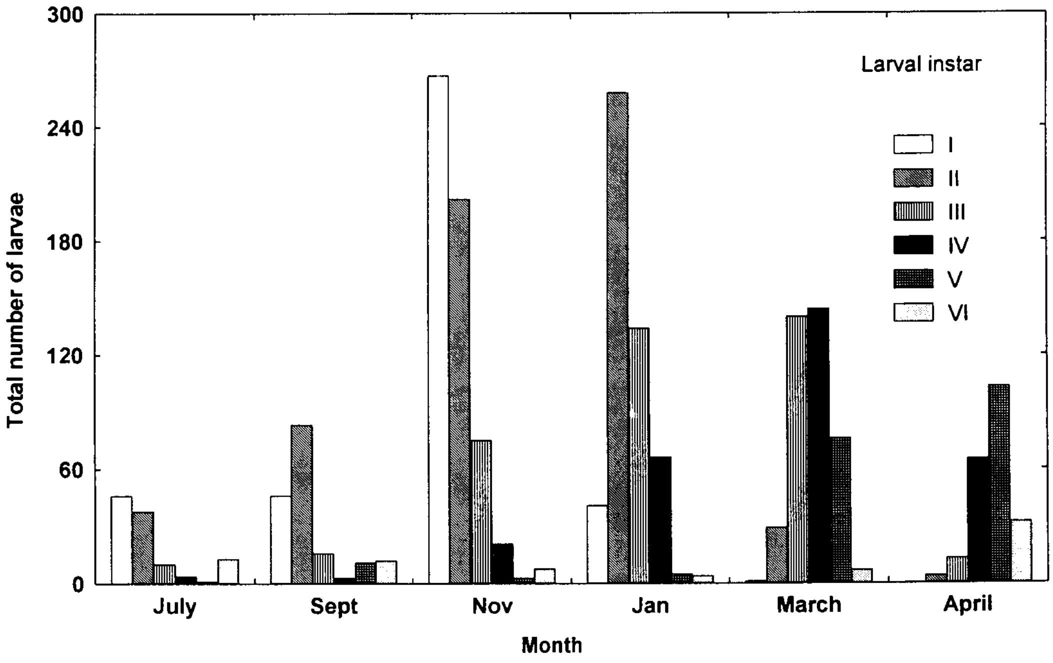

Fig. 4.2 Total number of each of the larval instars of *B. elongatus* in each of the months sampled.

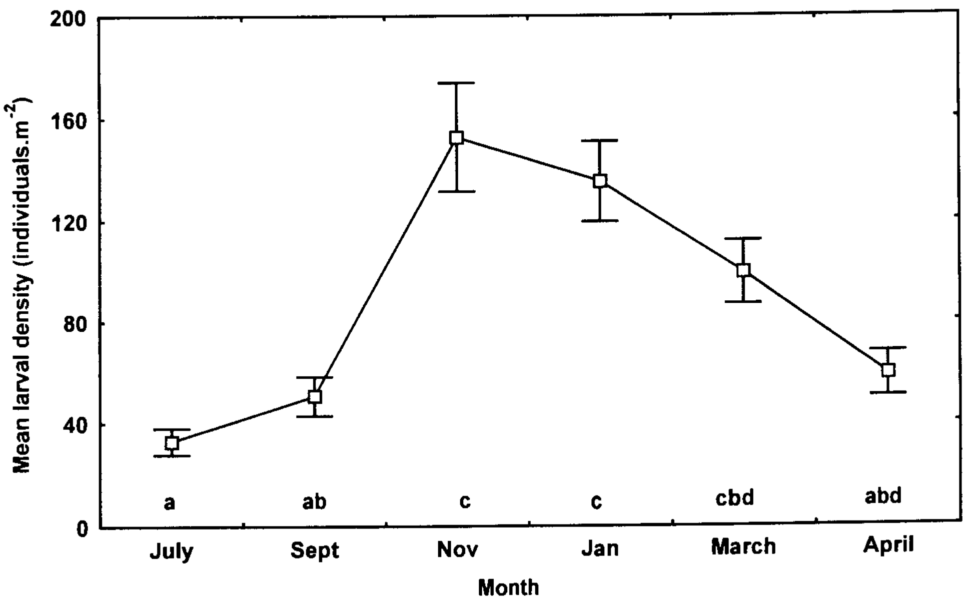

Fig. 4.3 Monthly changes in mean larval densities (mean ± S.E.) of *B. elongatus*. (Kruskal-Wallis statistic, $H = 59.15$, $P < 0.001$) (for each month $n = 40$ samples). Identical letters indicate months where larval densities do not differ significantly ($P < 0.05$) according to Dunn's multiple comparison.

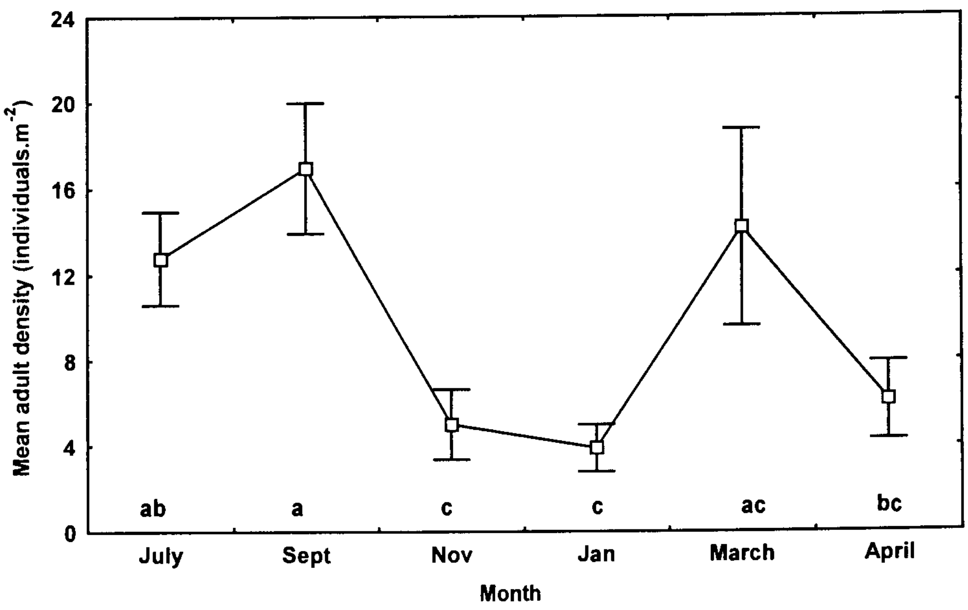

Fig. 4.4 Monthly changes in mean adult densities (mean ± S.E.) of *B. elongatus* (Kruskal-Wallis statistic, $H = 30.22$, $P < 0.001$) (for each month $n = 40$ samples). Identical letters indicate months where adult densities do not differ significantly ($P < 0.05$) according to Dunn's multiple comparison.

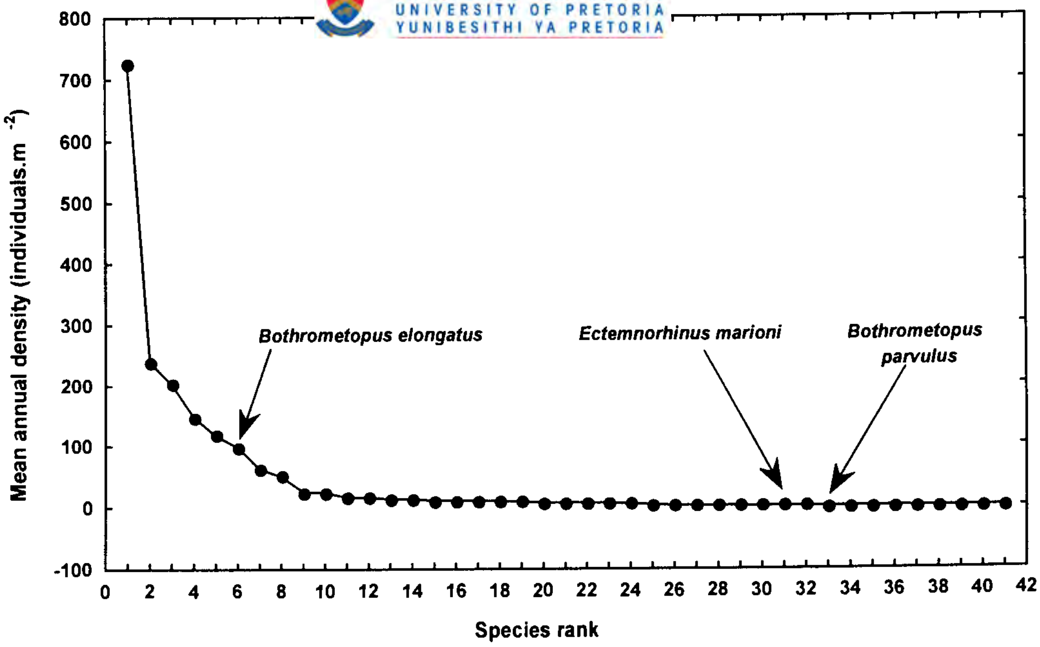

Fig. 4.5 Rank abundance curve of annual mean densities (individuals.m $^{-2}$) of all arthropods sampled in the fellfield habitat (J. Barendse, S.L. Chown & D.J. Marshall, unpublished data) (see **Discussion**).

Discussion

At an adult fresh mass of 1.55 ± 0.056 mg (mean ± S.E., $n = 20$) *Bothrometopus elongatus* is the smallest of the six weevil species found on Marion Island, and consequently in the epilithic biotope (Chown 1989, 1992, 1993a). Nonetheless, it is one of the largest arthropods occupying this habitat, with only *B. parvulus* (C.O. Waterhouse) and *E. marioni* (Curculionidae), *Pringleophaga marioni* Viette (Lepidoptera, Tineidae), and the predacious spider *Myro paucispinosus* Berland being larger (see Lawrence 1971; Crafford *et al.* 1986). Thus the high density of *B. elongatus* in fellfield is remarkable. This is further substantiated by a rank-abundance curve of annual mean densities recorded for all arthropod species in this habitat (Fig. 5). Amongst the eleven insect (including two other weevils), two spider, eight Collembola, and 21 mite species found at the Kerguelen Rise fellfield study site, *B. elongatus* was the sixth most abundant species. The other *Ectemnorhinus*-group weevil species, *Ectemnorhinus marioni* and *B. parvulus* were ranked 31st and 35th, respectively. Hence *B. elongatus* occurs at densities comparable to those of micro-arthropods in mid-altitude fellfield (the first five positions are taken by four mite and one collembolan species).

Preliminary investigations indicate that this high abundance is characteristic of *B. elongatus* throughout fellfield on Marion Island (A.G.A. Gabriel, S.L. Chown, R.D. Mercer & P.J.A. Pugh, unpublished data), but unusual compared with insects in most other habitats on the island (Gabriel 1999; Hänel 1999). Chown (1993a) also noted that, in terms of its desiccation resistance strategy, *B. elongatus* behaves somewhat more like the springtails investigated by Harrisson *et al.* (1991) than like other weevils. Thus, the small size of this species may make it remarkably different, in a variety of ways, to the other *Ectemnorhinus*-group weevils studied to date. Nonetheless, given its high abundance and relatively large body size, compared to all other arthropods in fellfield, it is clear that *B. elongatus* is an important species in this habitat, especially in terms of its energy use (see Blackburn & Gaston 1999 for discussion of energy use and body size). To date, few investigations of energy usage have been undertaken in fellfield on Marion Island (see Smith 1987).

Head capsule measurements suggest that *B. elongatus* has six larval instars, there being too few large individuals to substantiate a seventh instar. Chown & Scholtz (1989c) noted that *Ectemnorhinus marioni* shows similar life cycle flexibility, and such flexibility is not uncommon in a variety of sub-Antarctic species (Convey 1996a). Nonetheless, *B. elongatus* is similar to the other *Ectemnorhinus*-group weevils that have been examined to date. *Ectemnorhinus similis*, *B. randi* and *Palirhoeus eatoni* have seven larval instars while *E. marioni* has between five and seven instars (Chown & Scholtz 1989c; Chown 1993b).

Data on seasonal occurrence of the instars indicate a clear seasonal progression from a November peak in density of the first instar, to a peak in Instar VI density in April. Although these peaks are not absolute (i.e. there is a low abundance of late instar larvae in some other months), these data nonetheless suggest that *B. elongatus* completes a single generation *per annum*. Combined larval and the adult densities confirm this. Therefore the life cycle of *B. elongatus* can be summarised as follows: Adults eclose from pupae in late summer/early winter (April to July) and reach their maximum density in September. They are active during warm wet weather (Chown 1993a), when they feed, mate and lay eggs, with females maturing approximately three eggs at a time under these conditions. The eggs, within the norm in terms of size and number for adelognathan weevils (Howden 1995), hatch from July onwards. Larval eclosion reaches a peak in November, and development proceeds through six larval instars that feed exclusively on cryptogams (Chown & Scholtz 1989a). Pupation takes place from March/April onwards. Although there appears to be a peak in adult densities in March, densities at this time are not significantly different to those found in January and April.

As an indigenous sub-Antarctic weevil, the annual life cycle of *B. elongatus* may represent an uncommon life history strategy in the broader Antarctic region (Convey 1997). Although other indigenous insects from this region complete their life cycle in one year or less, for example the weevils *E. marioni* and *E. similis* (Chown & Scholtz 1989c) and the moth *Embryonopsis halticella* Eaton (Crafford & Scholtz 1986), the life-histories of most other Antarctic insects are hallmarked by flexibility rather than by set seasonal responses (viz. diapause and quiescence) (see Haderspeck & Hoffman 1990; Convey 1996b; and also Danks 1999 for a somewhat different view). Many of these latter species have extended life cycles lasting two or more years, characterised by overlapping generations, and seasonal activity peaks, though density peaks do not necessarily reflect single reproductive events. Such species include Continental and Maritime Antarctic Diptera (Convey & Block 1996), carabid beetles (*Amblystogenium* spp.) from the Crozet archipelago (Davies 1987) and from Îles Kerguelen

(Chevrier *et al.* 1997, but see Ernsting 1993 for a different seasonal response for *Oopterus soledadinus*, under the harsher environmental conditions of South Georgia), the diving beetle, *Lancetes angusticollis* from South Georgia (Block & Sømme 1983; Arnold & Convey 1998), and the moth *Pringleophaga marioni* from Marion Island (Chown & Scholtz 1989c; Crafford 1990).

In contrast, the life histories exhibited by many alien species that have established breeding populations in the sub-Antarctic tend to be more seasonal. These species often grow and reproduce relatively rapidly, completing several life cycles in a single year (a characteristic which probably assisted their successful establishment in the first place), followed by periods of extremely low activity. Examples of such species include the chironomid midge, *Limnophyes minimus* Meigen on Marion and Kerguelen Islands (Delettre & Cancela da Fonseca 1979; Hänel & Chown 1998), *Plutella xylostella* (Linnaeus) (Lepidoptera: Plutellidae) on Marion Island (Crafford & Chown 1990), and probably *Calliphora vicina* Robineau-Desvoidy (Diptera: Calliphoridae) on Marion and Kerguelen Islands (Chown & Language 1994; Chevrier *et al.* 1997). Hence these introduced species are rather unlike the majority of indigenous sub-Antarctic insect species that have extended life cycles, and are also different to those indigenous species, such as *B. elongatus*, which complete their life cycles in a single year.

Convey (1996b) suggested that the sub-Antarctic is a region characterised by relatively weak seasonal cues as a result of limited temperature variation, and that the life histories of insects occurring there are consequently relatively aseasonal. Although this does appear to be the case for many species, there are clearly a number of significant exceptions to this generalisation, as evidenced by *B. elongatus* and a variety of other indigenous and alien taxa. This diversity of life history strategies at once presents a useful opportunity for testing hypotheses regarding the influence of the environment on insect life histories, and grounds for concern regarding the impact of alien species at the islands. For example, Chown & Gaston (1999) have suggested that insects inhabiting short-lived habitats (such as carrion), and that have short generation times relative to the length of the growing season should show (1) a decrease in development time, (2) an increase in body size with increasing environmental harshness, and (3) reduced variation in voltinism. On the other hand, variation in voltinism should be more important, and body size clines should show a saw-toothed type pattern in species that have longer generation times relative to habitat durational stability.

In the second instance, the consistent difference in strategies between indigenous and alien species is especially significant in the context of climate change (mostly an increase in temperature and decline in precipitation) taking place at many of the sub-Antarctic islands (see Bergstrom & Chown 1999). Increased growth rate and development with temperature is usual in insects (see Honěk 1996). Thus an increase in temperature at the islands is likely to affect the life cycles of both indigenous (e.g. *Hydromedion sparsutum* and *Lancetes angusticollis* at South Georgia (Meyer-Arndt 1984; Haderspeck & Hoffmann 1990; Arnold & Convey 1998), and alien species (e.g. *Plutella xylostella* at Marion Island, see Crafford & Chown 1990). However, it seems likely, given the rapid generation time and overlapping generations of most alien species, and the longer life cycles of most indigenous species, that the alien species will be at a greater reproductive advantage. This advantage, together with the increased likelihood of propagule establishment predicted to occur with climate change at the islands (see Smith & Steenkamp 1990; Kennedy 1995; Chown *et al.* 1998), and the pronounced effect of alien species on indigenous ones (e.g. Ernsting *et al.* 1999) suggests that the effects of alien species are likely to become increasingly important in the terrestrial ecosystems of Southern Ocean islands.

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Chapter 5. Synthesis

> 'I am Kim. I am Kim. And what is Kim?' His soul repeated it again and again.
>
> He did not want to cry, - had never felt less like crying in his life, - but of a sudden easy, stupid tears trickled down his nose, and with an almost audible click he felt the wheels of his being lock up anew on the world without. Things that rode meaningless on the eyeball an instant before slid into proper proportion. Roads were meant to be walked upon, house to be lived in, cattle to be driven, fields to be tilled, and men and women to be talked to. They were all real and true – solidly planted upon the feet – perfectly comprehensible – clay of his clay, neither more nor less."
>
> **Rudyard Kipling – Kim**

Throughout this study, the central theme to emerge was that only quantitative community data can provide the resolution needed to adequately understand, monitor and conserve sub-Antarctic ecosystems. Up to now the collection of such data has largely been absent. The work represented in these chapters, though admittedly still lacking in aspects such as taxonomic resolution, or ignoring yet smaller organisms (such as tardigrades and eriophyid mites that were recorded in this study, but not quantified) has shown the value of systematic and quantitative surveys and the information these can yield on aspects such as biology of individual species, community processes and conservation biology, in the light of global change. At least initiatives in this direction are on the increase, especially with the growing interest in tourism in the Southern Ocean, and the implications this holds (e.g. Young 1995; Bergstrom & Chown 1999). Change in sub-Antarctic terrestrial ecosystems is inevitable, and in the case of arthropod and plant introductions to these islands, there is very little to be done about these changes (Gremmen 1997; Gremmen *et al.* 1998; Gremmen & Smith 1999). The only viable stance to take is that of observing the effects of past changes, and of increasing awareness in order to prevent further unnecessary introductions. Based on the findings in this thesis, the following points emerged as issues of further importance, and which deserve future attention:

1) An integrated approach, i.e. across habitats, taxonomic groups, regions and disciplines (e.g. physiology, ecology) can often provide far more valuable information than simply looking at specific issues in isolation. The sub-Antarctic region, due to its unique features, could allow a better understanding of local and regional community and assemblage processes than anywhere else in the world. This approach can also challenge or strengthen hypotheses that were based on previous research that had a more limited scope, or narrower focus.
2) The sub-Antarctic islands, though arguably some of the most pristine habitats remaining on earth, have also been affected by the presence of humans. This has especially been manifested in man's outstanding capacity as vector for the dispersal of various organisms alien to these islands (Bergstrom & Chown 1999). Given the low number of indigenous species of arthropods, their apparent generalist habits and the lack of biotic interactions,

introduced species may impact dramatically on natural occurring communities and ecosystems. Introduced species may provide selective forces previously absent from these systems (see Ernsting *et al.* 1999). This needs closer attention, especially where introductions are well documented (e.g. Brandjes *et al.* 1999). Furthermore, there is much room for work on arthropod life-histories, other than insects, especially for data collected over extended periods of more than a single year and on all life stages. This would be invaluable in assessing the differential responses of native and alien taxa under changing climatic conditions.

3) The numerous biogeographical enigmas revealed by this study need further attention. For example, the mites from the mesostigmatid family Cillibidae (see Chapter 3), an indicator taxon for all vegetated habitats, is a suspected human-assisted introduction (see Pugh 1994, 1997), because its Marion Island record is the first and only in the sub-Antarctic (Marshall *et al.* 1999). However, its ubiquitous occurrence and high abundance in all vegetated habitats seems surprising for a recent arrival. Alien insects are well known to have significant impacts on native arthropod communities either by affecting ecosystem function (e.g. Hänel & Chown 1998) or through biotic interactions (e.g. Ernsting *et al.* 1995; Chevrier *et al.* 1997). With further knowledge on biogeographical backgrounds of the mite faunas of Marion Island, further interesting patterns may become evident.
4) Similarly thorough quantitative studies down to the micro-arthropod level on other sub-Antarctic islands may shed light on the currently inexplicable patterns in community structure. Also, the variation in size and geological age of the various sub-Antarctic islands can be valuable for the testing of broad-scale evolutionary patterns (see Chown *et al.* 1998).

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"And in the end, the love you make
Is equal to the love you take ......"
The Beatles.