Patterns in the abundance and distribution of littoral and supralittoral arthropods on Marion Island

by

Richard Dennis Mercer

Submitted in partial fulfilment of the requirements for the degree
Master of Science (Entomology)
in the Faculty of Natural-, Agricultural- and Information Sciences
(Department of Zoology and Entomology)
University of Pretoria

March 2000

... to mum and dad

CONTENTS

PAGE

ACKNOWLEDGEMENTS

This thesis is the culmination of three years work which all started in April 1997. During this time I travelled from Marion Island to Mozambique making many new friends and regaining old ones. This page is especially for those people who shared in my thesis – whether they wanted to or not – who provided me with distractions and most importantly encouragement.

Firstly, thanks to Mum and Dad for providing me with the means to grasp opportunities that came along and for giving me the mental and financial support that has kept me going all these years. To the rest of the Mercer family – Andrew, Julie, Penny, Kelly and Jason – thanks for all the presents, talks and teasing.

A very special thanks to Jaco Barendse - my fellow Gogga on the Marion 54 team – for all the help in the field and the endless hours of painstaking sorting. A source of discussions, sanity, production videos, bacon sandwiches, Atchar Runipu, guitar lessons, music and coffee – thank you.

Thanks also to ...
... my boss, Prof Steven Chown, who managed to knead three papers out of me and taught me more than just how to write a thesis;
... to Dr David Marshall who introduced me to mites, taught me how to identify the little things and provided me with the background in littoral and supralittoral mite ecology in which many of the ideas in this thesis are rooted;
... my Marion 54 family, Raji the Gortex Guru, the M.I.T.I.E. team and Dr Philip Pugh - your humour, parties, data and discussions were always useful;
... to Dr Melodie McGeoch for statistical guidance, Marie Rösch for countless coffee breaks, encouragement and discussions, to Addo and the rest of the Polar Room;
... Kate Parr for being there the last few months to provide me with smiles, nourishment, encouragement and the occasional kick.

Financial and logistic support to Marion Island was provided by the Department of Environmental Affairs and Tourism, Directorate Antarctica and Islands (DEA&T, DAI), and home-based studies were financed through a National Research Foundation grant-holder linked bursary and a University of Pretoria merit bursary.

ABSTRACT

This study provides the first quantitative analysis of the littoral and supralittoral arthropod assemblages of sub-Antarctic Marion Island. Seventeen mite species (126 203 individuals) from 11 families were found on the shore at Macaroni Bay. Three families dominated the assemblages in both abundance and diversity: the Hyadesiidae, Ameronothridae and Halacaridae. Six insect species from three orders were found on the shore. Species richness increased from one in the littoral, to four and two species in the *Mastodia* and *Caloplaca* zones, respectively. The littoral, chironomid midge, *Telmatogeton amphibius* was the most abundant insect species, constituting 80% of all insects counted. Arthropod assemblages corresponded closely to the cryptogram dominated zonation patterns previously identified for the Marion Island shore. This clear association between arthropod and cryptogam zonation patterns provided a clear indication of habitat specificity in many of the species, and a quantitative analysis of habitat specificity on a species by species basis supported this tenet. The specificity of most species to the shore, which forms part of the epilithic biotope, is most likely a consequence of the considerable age of this biotope compared to the younger, post-glacial vascular vegetation. Tourist species, i.e. species transient to an assemblage, inflated species richness in zones and the distribution ranges of species across zones. It is suggested that previous, qualitative analyses of shoreline arthropod communities may have overestimated species ranges and richnesses because of the inclusion of tourist species. It is suggested that if a sound understanding of patterns in and processes underlying Antarctic arthropod assemblages is to be achieved, quantitative analyses must be expanded in the region.

In this study the spatial patterns of littoral and supralittoral arthropods from sub-Antarctic Marion Island are examined. Primary consumers were by far the most diverse group on the shore, with nine algivore and ten fungivore species from a total of 23 species. Positive species associations were found in the *Mastodia* and *Caloplaca* zones and positive abundance covariation in the *Verrucaria*, *Mastodia* and *Caloplaca* zones. There were no negative associations between any taxa, indicating that interspecific interactions on the shore are either minimal or absent. Significant interactions were related to the diversity of the respective habitats, with higher diversity resulting in higher levels of positive associations and abundance covariation. High levels of aggregation clearly demonstrated that species were not randomly distributed within habitats. Intraspecific aggregation was generally higher than interspecific aggregation in the five habitats and if competition was to occur it would most likely be among conspecifics. The absence of suitable biological information for species precluded further analyses of competition. However, if competitive interactions were found to occur between heterospecifics then coexistence would best be explained using the aggregated nature of superior competitors, allowing weaker competitors to

coexist in zones. Positive associations between species were attributed to favourable environmental conditions, the availability of limiting resources (e.g. shelter) and the structure of the dominant cryptogram species.

Body sizes, spanning five orders of magnitude (0.5 µg - 26 mg), were measured for 59 of the approximately 120 invertebrate species on Marion Island. Mass-length and fresh-dry mass relationships were calculated for orders, families and species (for those with sufficient data). A comparison of their slopes indicates that for prediction of body mass it may be useful to use regressions from the lowest taxonomic rank possible. Differences between the mass-length relationship for Marion Island insects (log mass = -4.294 + 3.151 log length) and other relationships on continental assemblages raises the questions as to the applicability of these results. This study should prove useful for estimating body sizes for other, similar taxa in the Antarctic and provide baseline information on an important species trait that seems to be changing with local and global environmental changes.

CHAPTER 1 GENERAL INTRODUCTION

1.1 RATIONALE

Current research on Marion Island is aimed at determining the distribution, abundance, body size and energy usage of all terrestrial macro- and meso-invertebrate species.. This project, along with others, falls under the Marion Island Terrestrial Invertebrate Ecology (M.I.T.I.E.) program and aims to quantify the fauna from all the major habitat types on the island. The littoral and supralittoral environment represents an important ecotone between the marine and terrestrial systems where a large proportion of the marine nutrients introduced onto the island are deposited and degraded (Smith 1977). Little is known about the invertebrates inhabiting the shores, the processes structuring the communities and the contributions they make to ecosystem functioning. This forms the major rationale for the current study.

A second reason for this work is to provide baseline data that can be used for future monitoring of local and regional changes. In the Antarctic, current research focus is on the effects that climate and humans have on the environment (Lewis Smith 1990; Gremmen 1997; Chown *et al.* 1998; Bergstrom & Chown 1999). On Signy Island (60°43'S, 45°38'W) extensive biological and environmental research programmes have provided a wealth of ecological information important for the assessment of both naturally and human-induced change (Lewis Smith 1990). The data collected in this study, and also from other studies within the M.I.T.I.E. framework, can be used for similar purposes.

Abiotic and biotic factors have a strong influence on the distribution of organisms on the shore and are responsible for the formation of the different zones. The littoral zone experiences marine conditions, is inundated with seawater with short periods of exposure to desiccation and has relatively low and stable temperatures. The converse is true of the supralittoral which is relatively dry, experiences short periods of inundation by seawater and freshwater, and has a broad temperature range. There is a continuum of conditions between these two extremes and together with biotic interactions (e.g. competition and predation) these determine the structure of local communities. Many studies have shown that marine organisms have upper distribution limits that are determined mainly by their tolerances to abiotic extremes and their lower distribution limits to the effects of competition (e.g. Mathieson & Nienhuis 1991; Davenport & MacAlister 1996). However, the converse has been proposed for terrestrial invertebrates (Pugh & King 1985; Pugh 1996), where the lower distribution limits are determined by tolerances to abiotic conditions and the upper limits determined mainly by biotic interactions. While the physiological tolerance limits of many terrestrial intertidal invertebrates are known (e.g. Sømme & Block

1984; Block & Convey 1995), little data gave evidence for the presence of biotic interactions in sub-Antarctic shoreline communities. To address these major goals I have adapted two main research aims:

> Aim 1 - To quantify the littoral and supralittoral invertebrate communities, to compare the zonation patterns based on invertebrate abundances to the cryptogram zonation patterns identified by de Villiers (1976), and to compare the communities on Marion Island with those of other sub-Antarctic islands.

> Aim 2 - To test the hypothesis that biotic interactions are stronger in the supralittoral than in the littoral through species associations, abundance covariation and species aggregation.

The third aim of this work was to provide body sizes for all the invertebrates on Marion Island. Despite the substantial literature on the invertebrates from the sub-Antarctic and Antarctic (see e.g. Block 1984; Greenslade 1990; Pugh 1993; Chown 1994; Convey 1997; Starý & Block 1998; Vernon *et al.* 1998; Davies & Melbourne 1999; Hänel & Chown 1999) no authors have presented species body sizes in an easily accessible format, despite the usefulness of doing so (Blackburn & Gaston 1994). Because of the difficult nature of weighing invertebrates in the field, and a strong need for estimating body sizes, it would be useful to have a series of mass-length relationships to enable weights to be calculated.

> Aim 3 - To collate body sizes for the invertebrate species on Marion Island, calculate mass-length relationships for the major taxonomic groups, and collate all this into an easily accessible format.

1.2 The Prince Edward Islands

1.2.1 Position, topography and geological history

The Prince Edward island group is located in the Southern Ocean with the nearest land, the French Crozet Archipelago, over 920 km to the east and South Africa over 2000 km to the north-west (see Fig. 1.1). Marion (46°54'S, 37°45'E), the larger of the two islands in the archipelago, has a surface area of 290 km² and a maximum elevation of 1230 m. Prince Edward (46°38'S, 37°57'E), only 20 km north-east of Marion, is almost seven times smaller with a maximum elevation of 672 m. Both islands have a central highland surrounded by coastal plains which vary in width from a few hundred metres to five kilometres.

The islands are the summits of two closely related, coalescing shield volcanoes with the oldest exposed lavas extruded approximately 276 000 years ago (Kable *et al.* 1971; Verwoerd 1971). Marion has been subject to a number of glacial episodes with the most recent, estimated at 30 000 to 15 000 BP, coinciding with the global Pleistocene glaciation (Hall 1990). However, no evidence of glaciation has been found on Prince Edward (Schalke & van Zinderen Bakker 1971), suggesting that it may have served as an ice-free refuge. The islands are presently 2° north of the Antarctic Convergence, making climatic conditions more temperate than most other sub-Antarctic islands lying south of the convergence (e.g. South Georgia Island and Bouvetøya).

1.2.2 Climate

The Prince Edward Islands have a cool, hyperoceanic climate. The temperature regime is closely related to that of the surrounding ocean due to the islands small landmass, low incidence of sunshine and high winds (see Schultze 1971; Gremmen 1981; Smith 1987). Based on data collected between 1948 and 1965 Schultze (1971) gave a detailed account of the climate and pointed out the following outstanding features:

a) Low mean annual air temperature (~5°C) with little diurnal (~1.9°C) or seasonal variation. The coldest month is August (~3.2°C) and the warmest February (~7.3°C);
b) High relative humidity with an annual mean screen value approximately 85%;
c) Abundant precipitation (>2500 mm per annum) mainly in the form of rain, distributed evenly throughout the year;
d) A high degree of cloud cover which implies a low percentage of possible sunshine duration, the annual mean is 30% of the maximum possible;
e) Strong predominantly westerly winds, regularly reaching gale force (>55 km/h) for a third of the year.

Climatic conditions recorded daily at the meteorological station, on the north-western section of the Marion Island, refer to the macroclimatic conditions as recorded in the Stevenson Screen. Although climatic conditions appear relatively uniform with minor seasonal fluctuations invertebrates exhibit seasonal patterns (see Barendse 2000). Microclimate conditions are extremely variable over the island, even for sites within a few kilometres of the weather station (Chown & Crafford 1992; Blake 1996), and this may influence patterns of species abundance and distribution.

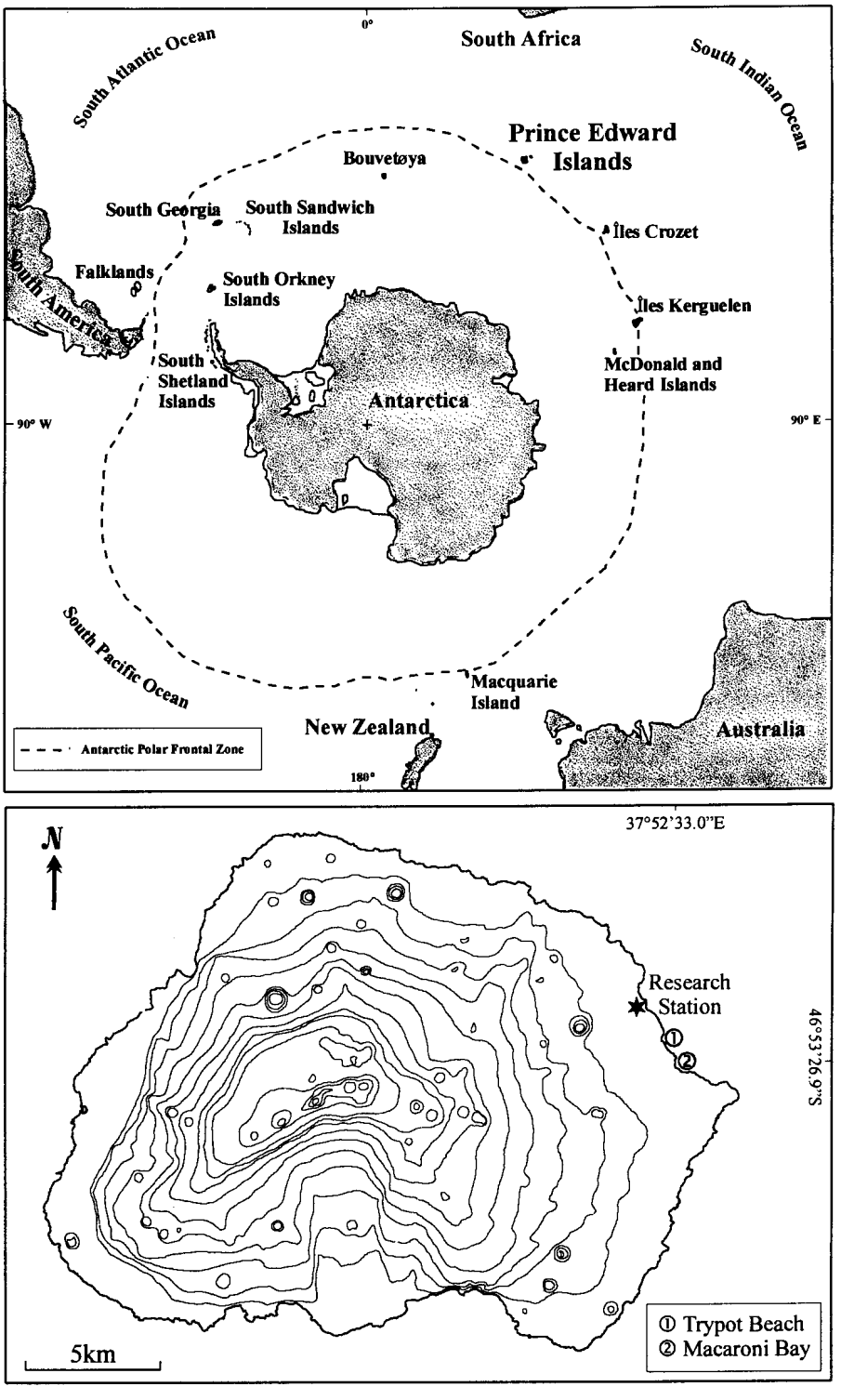

FIG 1.1 A map of the South Polar Region showing the Prince Edward Islands in relation to the other sub-Antarctic islands and oceanographic features and the approximate location of Macaroni Bay and the research station on Marion Island.

1.3 THE SHORE ENVIRONMENT

The 72 km coastline of Marion has no headlands or bays which can protect the coast to form a sheltered shore. de Villiers (1976) considered the entire littoral environment to be one of the most exposed shorelines in the world, although he points out that this is a qualitative description which lacks any quantitative basis. The western shores of Marion do, however, experience some of the harshest conditions known in the world. The vegetation complexes associated with these sections of the island may give a partial quantification of the severity of the region. For example the *Crassula moschata*, salt-spray complex on the more exposed western coastline is much wider than on the more sheltered eastern coastline (see Gremmen 1981 for details of the vegetation complexes).

de Villiers (1976) provided the first ecological study of shoreline communities on Marion Island, and divided the shores into several broad categories:

a) *Vertical cliffs*

These range in height from a few metres to over 30 m and dominate a large proportion of the coastline.

b) *Broken shores*

Boulder lined shores are found at the bases of some of the cliffs. The gradation in boulder shape and texture is concomitant with size and degree of exposure. Where smallest (Ø < 10 cm) the pebbles are rounded and polished and form stony beaches. These small pebbles are heavily pitted and many of the smaller invertebrates use these pits as refugia. Larger boulders (Ø up to 100 cm) are also rounded, but as a result of increased stability are covered by algae and lichens. Very large boulders in excess of several metres are frequently rough and angular and have rich growths of intertidal organisms. A comparison of boulders of similar size on the west and east coast illustrates the consistently severe wave action on the west coast, since the boulders there are less angular and have a sparser covering of cryptograms.

c) *Sloping unbroken rock*

This is an uncommon shore type on Marion Island. The basic pattern of sub-Antarctic zonation (after Knox 1994) is well illustrated on this shore type.

d) *Low reefs*

These extend seawards as low rocky shelves which are frequently awash, often occurring at the bases of cliffs.

e) *Sand and shingle beaches*

These are rare and periodically eroded away by storms. There is one sandy beach composed of fine volcanic particles and two shingle beaches on Marion.

Sea surface temperatures are recorded daily from Gunners Point. These data provide an indication of seasonal variation. The results below are taken from 15 years data collected between 1951 and 1965. The sea surface temperature is warmest in late summer, February and March (6.1°C) and coldest in late winter, August and September (4.0°C) with a mean annual range of 2.1°C. Monthly ranges are narrow with a mean annual range (between the maximum and minimum) of 3.2°C. The constant temperature of the sea water produces an aseasonal microclimate. However semi-diurnal, that is circa-tidal, changes on the shore may be extreme (e.g. being exposed to air and being submerged).

During the winter months supralittoral pools may have a thin layer of surface ice, and snow sometimes collects between boulders and pebbles (personal observation). However, there is no build up of ice or snow in the littoral zones as a consequence of the stable sea temperatures, and no permanent ice develops. The tidal range at Marion Island is very small, calculated at around 70 cm during spring tides (de Villiers 1976). In spite of this limited tidal range the shore zonation patterns are well developed and follow closely the patterns observed on other sub-Antarctic islands (de Villiers 1976; Knox 1994). Swell height at Marion Island overrides the tidal range by several metres, particularly on the exposed western coast, and it is the raising of effective tidal heights by wave action which results in much of the zonation. Swell heights from the sheltered eastern coastline are very different from the more exposed western shores, but data are available only from the meteorological staff at the research station. Analysis of data from one annual cycle (March 1972 to February 1973) has shown that swell heights are < 1 m for 67% of the time (de Villiers 1976). Another important factor is the periodicity of extreme conditions such as violent storms or extended periods of exceptional calm. de Villiers (1976) found that swells attained a height above 2 m at least once a month throughout the year. Violent storms have a large effect on the beaches and can move large (Ø > 40 cm) boulders from the sublittoral to the lower supralittoral (personal observation). The sand beaches on Marion are also constantly changing shape and size as rough swells wash away and redeposit sand.

1.4 BIOTA

Marion Island has been described as having a tundra-type terrestrial biome (Crafford *et al.* 1986) with six community complexes and 41 plant communities (Gremmen 1981). Only 40 species of vascular plants, 17 of them introduced (Chown *et al.* 1998), have been recorded from Marion. A further 72 moss, 36 hepatic and approximately 100 lichen species have also been recorded (Crafford 1987). Phytogeographically, the vegetation has its closest affinities within the South Ocean Indian Province (previously the Kerguelen Biogeographical Province), comprising the Crozet and Kerguelen archipelagos, and Heard Island (Gremmen 1981; Lewis Smith 1984; Crafford *et al.* 1986).

The terrestrial environment on Marion is heavily influenced by the surrounding ocean - indirectly through the faeces of birds and seals (Smith 1977), and directly by the input of nutrients from sea spray and marine products (Crafford & Scholtz 1987). There are 26 species of nesting birds on Marion which play an important role in the introduction of energy and nutrients onto the island (Smith 1977). The 14 surface nesting species are estimated to void 3615 tons (dry mass) of guano per annum, 98% of this from the four penguin species (Burger *et al.* 1978). Three species of seals breed on Marion Island, namely the Southern Elephant seal (*Mirounga leonina*) and two fur seal species (*Arctocephalus tropicalis* and *A. gazella*). The seals have a large effect on the surrounding ecosystem, by influencing the topography (e.g. wallow formation) and introducing nutrients in the form of faeces and moulted skin, which influences the distribution and density of the invertebrate faunas (Panagis 1985).

There are no indigenous terrestrial mammals on Marion Island. Feral house mice (*Mus musculus*) were introduced approximately 170 years ago through sealing activities and ship wrecks. The mice, now well established on the island, have a considerable effect on the functioning of the island ecosystem (Huyser *et al.* 2000; Bergstrom & Chown 1999). Their principal prey, *Pringleophaga marioni* (Lepidoptera: Tineidae), which constitutes 50% of their diet, is an important detritivore in the ecosystem, processing up to 1500 tons of litter annually (Crafford 1990). The removal of a large proportion of the decomposer biomass by the mice has an indirect effect on the mineralization and decomposition processes on the island. However, the introduced midge, *Limnophyes minimus* (Chironomidae), may have taken over part of that role (see Hänel & Chown 1998).

Approximately 120 invertebrate species have been recorded from Marion Island to date (Table 1.1), almost twice as many as were known up until the early 1990's. The reason for the sudden increase in known invertebrate taxa is that attention is now being paid to the micro-invertebrates (e.g. mites and springtails). Mites and springtails are the dominant invertebrates in the Antarctic and maritime Antarctic (Block 1985; Pugh 1995) and on Marion Island they form important links in terrestrial food webs. An increased knowledge of their taxonomy, distribution, abundance and biologies will add greatly to the understanding of the functioning of the terrestrial systems on Marion and other sub-Antarctic islands.

1.5 Comparison of Macaroni Bay with other beaches

The aim of this section is to compare the study site at Macaroni Bay with other beaches which were sampled during the year. Two separate beaches were sampled at Trypot Beach (approximately 900 m south of the research station) but the data are not complete and thus not incorporated into the overall study. However, qualitative descriptions of these beaches together with notes on other sections of the

Marion Island coastline will provide information which may be useful in understanding the distribution of arthropods on the shores.

TABLE 1.1 Numbers of free-living terrestrial invertebrates on the Prince Edward Island archipelago (Crafford *et al.* 1986; Chown *et al.* 1998; Gabriel 1999; Marshall *et al.* 1999).

Group	No. of species 1986	No. of species 1999
Phylum Arthropoda		
Class Insecta	27	35 §
Class Collembola	13	16
Class Arachnida		
Order Araneae	4	4
Order Acari	19	> 60
Phylum Annelida		
Class Oligochaeta (earthworms)	3	3
Phylum Mollusca		
Class Gastropoda (slugs and snails)	2	2
Total	68	120

§ - includes 16 alien species

The main Trypot beach (referred to as T_1) is a pebbled beach with a shallow gradient. The beach is exposed to wave action and between tide marks the beach becomes quite steep. The boulders range in size from a few centimetres to > 20 cm in diameter. This is the most biotically influenced beach that was examined, with kelp and other sublittoral algae washed up onto the beach during heavy storms (Crafford 1984). Elephant seals (*Mirounga leonina*) and Fur seals (*Arctocephalus gazella* and *A. tropicalis*) use the beach during for moulting and breeding, providing nutrients from their shed skin and faeces. Their movements on the beach physically break down the wrack beds and aid in increasing decomposition rates. Two penguin species are found utilising the shore. King Penguins (*Aptenodytes patagonicus*) use the beach during the moulting season but do not breed here and Gentoo Penguins (*Pygoscelis papua*) use the beach as an entry point to the sea. The combination of wave action and animal movement makes the pebbles rub together, producing smooth and polished surfaces. An unusual feature of the pebbles on the

shores of Marion Island is the heavy pitting probably caused by air bubbles present in the volcanic lava during cooling. These pits range in size up to 10 mm in diameter and provide refugia to small invertebrates which would otherwise be squashed when the pebbles turn (personal observation)

The second Trypot Beach (referred to as T_2) is approximately 100 m from the main beach. It has a steeper slope than T_1, with larger pebbles which range from 20 cm up to large embedded rocks. The beach has a narrow entrance, which together with the angle of the channel shelters it against the predominant swell direction. Because the beach is a lot smaller, steeper and less accessible it receives less marine debris, and fewer animals use the beach, making it less biotically influenced than T_1. The beach is also less dynamic than T_1 because: (1) the pebbles are larger and require more force to make them move, (2) the beach is sheltered to some extent from wave action and (3) there are fewer seals to disturb the beach. Thus there is more cryptogram growth on the boulders with distinct *Caloplaca* sp. and *Mastodia* sp. lichens on the supralittoral rocks.

The substrate at the Macaroni Bay sampling site is highly stable with no pebbles or boulders. The shore is more exposed than the other two beaches and receives almost maximum wave action. However, this is still reduced compared to the wave action on the exposed western shores. The stability of the underlying basalt rock allows algae and lichens to colonise then effectively, with littoral zones having almost 100% cover. The shore, although devoid of potentially mobile rocks, still has a high level of disturbance. During heavy swells the fronds of the Bull Kelp (*Durvillaea antarctica*) wash extensively back and forth across the algae, disturbing the shoreline communities and stunting algal growth (see Kenny & Haysom 1962; Pugh & Davenport 1997). Kelp deposition on the shore is minimal and wrack beds do not form in the supralittoral. The only large animals to regularly use the shore are Lesser Sheathbills (*Chionis minor marionensis*), Imperial Cormorants (*Phalacrocorax atriceps*) and a few fur seals.

There is an apparent gradient of stability and biotic influence across the three beaches (see Table 1.2) but this cannot at this stage be quantified. The difference between the beaches is evident in their respective faunas and cryptogram coverage. T_2 has patches of the yellow lichen *Caloplaca* sp. and *Mastodia* sp. growing in the supralittoral, while T_1 is almost devoid of supralittoral cover. Large rocks in the lower littoral are covered by red algae (de Villiers 1976). The comparison of the three beaches is not the main direction of this thesis but forms part of another study. I have included the descriptions and species richness just to emphasise that the Macaroni Bay study site is not typical of Marion and not necessarily representative of all shores types.

TABLE 1.2 A summary of the three shores examined between May 1997 and April 1998. Data relating to species number and density are taken only from the littoral environment and excludes the supralittoral.

	Main Trypot (T_1)	**Small Trypot (T_2)**	**Macaroni Bay**
substrate stability	low	medium	high
% cover	low	medium	high
eutrophication	high	medium	low
exposure	medium	low	high
# mite species	12	16	4
# insect species	2	8	1
densities (qualitative obs)	low	low	high

1.6 REFERENCES

Barendse, J. (2000) *Patterns in the distribution and abundance of terrestrial arthropods on sub-Antarctic Marion Island*. MSc Thesis, University of Pretoria

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

Blake, B.J. (1996) *Microclimate and prediction of photosynthesis at Marion Island*. MSc Thesis, University of the Orange Free State

Blackburn, T.M. & Gaston, K.J. (1994) The distribution of body sizes of the world's bird species. *Oikos* 70:127-130

Block, W. (1984) Terrestrial microbiology, invertebrates and ecosystems. In: Laws R.M. (ed) *Antarctic Ecology, Vol 1*. Academic Press, London, pp. 163-236

Block, W. (1985) Arthropod interactions in an Antarctic terrestrial community. In: Siegfried, W.R., Condy, P.R., Lewis, R.M. (eds) *Antarctic nutrient cycles and foodwebs*. Springer-Verlag, Berlin, pp. 614-619

Block, W. & Convey, P. (1995) The biology, life cycle and ecophysiology of the Antarctic mite *Alaskozetes antarcticus*. *Journal of Zoology* 236:431-449

Burger, A.E., Lindeboom, H.J. & Williams, A.J. (1978) Mineral and energy contributions of guano of selected species of birds to the Marion Island terrestrial ecosystem. *South African Journal of Antarctic Research* 8:87-99

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

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

Chown, S.L., Gremmen, N.J.M. & Gaston, K.J. (1998) Ecological biogeography of Southern Ocean islands: species-area relationships, human impacts and conservation. *American Naturalist* 152:562-575

Convey, P. (1997) How are the life history strategies of Antarctic terrestrial invertebrates influenced by extreme environmental conditions. *Journal of Thermal Biology* 22:429-440

Crafford, J.E. (1984) Life cycle and kelp consumption of *Paractora* (Diptera: Helcomyzidae): A primary decomposer of stranded kelp on Marion Island. *South African Journal of Antarctic Research* 14:18-22

Crafford, J.E. (1987) *The Lepidoptera of the Prince Edward Islands (46°54'S, 37°45'E): ecology and zoogeography*. Msc Thesis, University of Pretoria

Crafford, J.E. (1990) The role of feral house mice in the ecosystem functioning on Marion Island. In: Kerry, K.R. & Hempel, G. (eds) *Antarctic ecosystems. Ecological change and conservation.* Springer-Verlag, Berlin, pp. 359-364

Crafford, J.E. & Scholtz, C.H. (1987) Phenology of stranded kelp degradation by the kelp fly *Paractora dreuxi mirabilis* (Helcomyzidae) at Marion Island. *Polar Biology* 7:289-294

Crafford, J.E., Scholtz, C.H. & Chown, S.L. (1986) Insects of sub-Antarctic Marion and Prince Edward Islands; with a bibliography of Entomology of the Kerguelen biogeographical Province. *South African Journal of Antarctic Research* 16:42-84

Davenport, J. & MacAlister, H. (1996) Environmental conditions and physiological tolerances of intertidal fauna in relation to shore zonation at Husvik, South Georgia. *Journal of the Marine Biological Association of the United Kingdom* 76:985-1002

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

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

Gabriel, A.G.A. (1999) *The systematics and ecology of the Collembola of Marion Island, sub-Antarctic.* MSc Thesis, University of Durban-Westville

Greenslade, P. (1990) Notes on the biogeography of the free-living terrestrial invertebrate fauna of Macquarie Island with an annotated checklist. *Proceeding of the Royal Society of Tasmania* 124:35-50

Gremmen, N.J.M. (1981) *The vegetation of the sub-Antarctic Islands Marion and Prince Edward.* Dr W. Junk, The Hague

Gremmen, N.J.M. (1997) Changes in the vegetation of sub-Antarctic Marion Island resulting from introduced vascular plants. In: Battaglia, B., Velencia, J. & Walton, D.W.H. (eds) *Antarctic communities: species, structure and survival.* Cambridge University Press, Cambridge, pp. 417-423

Hall, K.J. (1990) Quaternary glaciations in the Southern Ocean: sector 0° Long. – 180° Long. *Quaternary Science Reviews* 9:217-228

Hänel, C. & Chown, S.L. (1998) The importance of a small, alien macro-invertebrate on a sub-Antarctic terrestrial ecosystem: *Limnophyes minimus* Meigen (Diptera, Chironomidae) at Marion Island. *Polar Biology* 20:99-106

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

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

Kable, E.J.D., Erlank, A.J. & Cherry, R.D. (1971) Geochemical features of lavas. In: van Zinderen Bakker, E.M., Winterbottom, J.M. & Dryer, R.A. (eds) *Marion and Prince Edward Islands: report on the South African Biological and Geological Expedition 1965-1966*. A.A. Balkema, Cape Town, pp. 78-88

Kenny, R. & Haysom, N. (1962) Ecology of rocky shore organisms at Macquarie Island. *Pacific Science* 16:245-263

Knox, G.A. (1994) *The biology of the Southern Ocean*. Cambridge University Press, Cambridge

Lewis Smith, R.I. (1984) Terrestrial plant biology of the sub-Antarctic and Antarctic. In: Laws, R.M. (ed) *Antarctic Ecology Vol. 1*. Academic Press, London, pp. 61-162

Lewis Smith, R.I. (1990) Signy Island as a paradigm of biological and environmental change in Antarctic terrestrial ecosystems. In: Kerry, K.R. & Hempel, G. (eds) *Antarctic ecosystems. Ecological change and conservation*. Springer-Verlag, Berlin, pp. 32-50

Marshall, D.J., Gremmen, N.J.M., Coetzee, L., O'Connor, B.M., Pugh, P.J.A., Theron, P.D. & Ueckermann, E.A. (1999) New records of Acari from the sub-Antarctic Prince Edward Islands. *Polar Biology* 21:84-89

Mathieson, A.C. & Nienhuis, P.H. (1990) *Ecosystems of the world 24 - Intertidal and littoral ecosystems*. Elsevier, Amsterdam

Panagis, K. (1985) The influence of elephant seals on the terrestrial ecosystem at Marion island. In: Siegfried, W.R., Condy, P.R., Lewis, R.M. (eds) *Antarctic nutrient cycles and foodwebs*. Springer-Verlag, Berlin, pp. 173-179

Pugh, P.J.A. (1993) A synonymic catalogue of the Acari from Antarctica, the sub-Antarctic Islands and the Southern Ocean. *Journal of Natural History* 27:323-421

Pugh, P.J.A. (1995) Air-breathing littoral mites of sub-Antarctic South Georgia. *Journal of Zoology, London* 236:649-666

Pugh, P.J.A. (1996) Using artificial substrata to monitor how cryptofaunal acari colonise littoral algae on sub-Antarctic South Georgia. *Acarologia* 37:189-200

Pugh, P.J.A. & Davenport, J. (1997) Colonisation vs. disturbance: the effects of sustained ice-scouring on intertidal communities. *Journal of Experimental Marine Biology and Ecology* 210:1-21

Pugh, P.J.A. & King, P.E. (1985) The vertical distribution of the British intertidal Acari - the non halacarid fauna (Arachnida: Acari). *Journal of Zoology, London* 207:21-33

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

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

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

Smith, V.R. (1987) The environment and biota of Marion Island. *South African Journal of Science* 83:211-220

Sømme, L. & Block, W. (1984) Ecophysiology of two intertidal mites at South Georgia. *Oikos* 42:276-282

Starý, J. & Block, W. (1998) Distribution and biogeography of oribatid mites (Acari: Oribatida) in Antarctica, the sub-Antarctic islands and nearby land areas. *Journal of Natural History* 32:861-894

Vernon, P., Vannier, G. & Trehen, P. (1998) A comparative approach to the entomological diversity of polar regions. *Acta Oecologia* 19:303-308

Verwoerd, W.J. (1971) The climate change of Marion Island. In: van Zinderen Bakker, E.M., Winterbottom, J.M. & Dryer, R.A. (eds) *Marion and Prince Edward Islands: report on the South African Biological and Geological Expedition 1965-1966.* A.A. Balkema, Cape Town, pp. 40-62

CHAPTER 2 ARTHROPOD ZONATION ON A MARION ISLAND ROCKY SHORE: A QUANTITATIVE APPROACH [1]

2.1 INTRODUCTION

Coastal shores are not sharp boundaries. Rather, they represent a gradual transition between the marine and terrestrial environments. Zonation patterns are characteristic of such areas and nowhere are they more evident than on rocky shores. Intertidal zonation patterns first attracted scientific interest in the 1840's (Ricketts & Calvin 1968), and since then much work has focused on describing these patterns and understanding the processes behind their formation (Lewis 1964; Stephenson & Stephenson 1972; Mathieson & Nienhuis 1990). Most studies have only examined portions of the intertidal community and have tended to concentrate on the larger organisms of marine origin. Smaller invertebrates, most notably the Acari, are often overlooked or ignored because of their small size, cryptic nature and difficult taxonomy (Luxton 1990a). In consequence, few studies have examined the Acari on coastlines (but see Pugh & King 1985a, 1985b; Kronberg 1988; Pugh & King 1988; Luxton 1990a, 1990b).

In keeping with this trend, most investigations of the ecology of sub-Antarctic shores have focussed on the macrobiota (de Villiers 1976; Smith & Simpson 1985; Simpson *et al.* 1995; Pugh & Davenport 1997), and in some cases the physiology of selected invertebrate species (Sømme & Block 1983; Davenport & MacAlister 1996; Davenport *et al.* 1997). While the distribution of arthropods has also been investigated (e.g. Bellido 1981; Pugh & Bartsch 1993; Pugh & MacAlister 1994; Pugh 1995, 1996), with some of these studies demonstrating clear zonation patterns, most of this work has been essentially qualitative and descriptive. In sharp contrast, both Usher *et al.* (1982) and Underwood (1996) have called for quantitative ecological investigations. These are essential if the processes structuring littoral communities are to be fully comprehended (Kronberg 1988; Lively *et al.* 1993; Underwood & Chapman 1996).

This is certainly true of sub-Antarctic islands, where quantitative studies of shoreline, arthropod communities are either scarce or often concern single taxonomic groups (e.g. oribatid mites, Bellido 1981). Thus a general understanding of the littoral and supralittoral environments in the sub-Antarctic, and comparisons between these remote systems, and those commonly found on continents are largely lacking, despite the obvious advantages of such work (see for example Davenport & Stevenson 1998),

[1] ms. submitted to *Polar Biology*

and the importance of these habitats in terms of species richness and ecosystem processes in the sub-Antarctic (Smith 1977; Crafford & Scholtz 1987). This is especially true for the Prince Edward Islands.

Early work on Marion Island included a preliminary account of the shores (Fuller 1967), and descriptions of the animals found on them (e.g. Engelbrecht 1974). de Villiers' (1976) study was the first to provide a comprehensive classification of the shores on Marion Island and described zonation patterns based on algae and lichens. Later studies focused on the biology of individual species (Crafford 1984), the influences of invertebrates on the decomposition of marine debris (Crafford & Scholtz 1987), feeding biologies of a few predators (Blankley & Grindley 1985), and the physiology of selected species (Chown & van Drimmelen 1992; Chown 1993a; Crafford & Chown 1993; Chown *et al.* 1997; van der Merwe *et al.* 1997). Thus, no studies have, to date, examined arthropod assemblage structure and zonation on the shores of Marion Island.

In this study, we therefore provide the first quantitative investigation of shore zonation patterns for arthropod assemblages on Marion Island, and the first such quantitative analysis of a complete arthropod assemblage for any sub-Antarctic island (see Bellido 1981; Travé 1981, 1982 for quantitative analyses of shoreline oribatid and collembolan assemblages). We also examine the extent of the correspondence between the arthropod zonation patterns and those described, on the basis of cryptogam distributions, by de Villiers (1976). In addition, we compare species distribution patterns across the shore at Marion Island with those documented on other sub-Antarctic islands. Finally, we also demonstrate the importance of quantitative data for meaningful estimates of species ranges across the shore and the species richness of each of the shore zones.

2.2 Methods

Fieldwork was carried out between May 1997 and May 1998 at Macaroni Bay on Marion Island (one of two islands forming the Prince Edward Islands, see Smith 1977 for general information on the islands and their biota). The northern section of Macaroni Bay (GPS location: 46°53'26.9"S, 37°52'33.0"E), on the sheltered eastern coastline, has a sloping (approximately 12°), unbroken rocky shore that displays a zonation pattern typical for Marion Island (de Villers 1976) and not unlike the general Antarctic zonation pattern described by Knox (1994). Although such sloping shores are relatively uncommon on Marion Island (de Villiers 1976; personal observation), they are relatively easy to sample and can be readily compared with other littoral and supralittoral studies from other sub-Antarctic islands (e.g. Bellido 1981).

Five zones (three littoral and two supralittoral) were readily distinguished based on the presence/absence of selected cryptogam species, and these corresponded to the zonation patterns described by de Villiers (1976). The Red zone, just above the upper limit of the kelp, *Durvillaea*

antarctica, is completely covered by red algae and represents the lower littoral and the lower-most habitat sampled. The mid-shore is dominated by members of the rhodaphyte genus *Porphyra* and forms the *Porphyra* zone. The *Verrucaria* zone is the first of the lichen-dominated zones, marking the upper-shore and falling within the supralittoral. This zone is predominantly dark grey to black as a result of the continuous lichen encrustation. A dark-green foliose lichen (*Mastodia* sp.) dominates the lower and mid-supralittoral and gives this zone its name. The uppermost supralittoral zone is covered by bright yellow crustose lichens of the genus *Caloplaca* and is the final zone before the onset of closed, terrestrial, vascular vegetation.

Six transects were marked out, stretching from the lower littoral to the upper supralittoral. Sampling was done bimonthly (June, August, October, December, February and April) with one transect sampled per month. All samples were collected on the same day within a five-day period over spring tide. A 1 m^2 sampling grid (sub-divided into 100 0.1 x 0.1 m squares) was randomly placed within each zone, and this provided 100 possible sampling positions from which 10 were randomly selected and collected. Samples were taken by scraping the algae or lichen (depending on the zone) from within a circular tube down to bare rock. Different sampling areas (∅ between 40 mm and 85 mm) were used for different zones to accommodate the high volumes of material. Samples were preserved in 70% ethanol.

Mites and insects (and a single oligochaete species in the lower shore) were hand-sorted from the samples and counted. Although labour intensive, this method was selected over others because it provided the highest level of extraction accuracy. Trials showed that heat-extraction processes dried out the algae too quickly, and hyper-saline flotation methods would not dislodge small mites caught up in filamentous algae. The *Verrucaria* and *Caloplaca* also required comminution because the smaller mites were often wedged between the thalli. By hand-sorting the material we were able to keep our extraction process consistent between the five habitats and were sure to have extracted > 99% (a repeated measures estimate) of all micro-arthropods from the samples. Identification was done down to the lowest possible taxonomic level, mostly down to genus and species. Some species were not readily distinguishable (even as morphospecies) and these were counted together and combined into supra-specific taxa. These included the Rhodacaridae and Tydeidae, as well as *Hyadesia kerguelensis* and *Hyadesia subantarctica* that were combined under *H. kerguelensis*, and *Rhombognathus auster*, if present, which was counted as *Isobactrus magnus*.

To examine the changes in community structure on the shore a non-parametric, multivariate approach was employed, based on methods described by Clarke (1993), Dufrêne & Legendre (1997) and van Rensburg *et al.* (1999). Species densities were pooled across months to reduce the data set before analysis and to remove the possible effects of seasonality. Non-metric multidimensional scaling (MDS) using PRIMER v4.0 (Clarke & Warwick 1994) was used to obtain an ordination of the samples. Prior to

analysis, sample abundances were double square root transformed to weight common and rare species equally (Clarke & Warwick 1994). Analyses of similarity (ANOSIM, Clarke 1993) were used to test for significant differences between sample groupings. The R-value provided by the ANOSIM tests the null hypothesis that there is no significant difference between groups of sites.

Characteristic species, i.e. species specific to a given zone or set of zones, were identified using the Indicator Value Method (IndVal - Dufrêne & Legendre 1997). Indicator species can be defined as the most characteristic species of a group of sites, being found in a single group and present in the majority of the sites belonging to that group (Dufrêne & Legendre 1997). The IndVal technique combines a species' abundance with its frequency of occurrence and expresses this as the degree to which the species fulfils the criteria of specificity and fidelity. Species were regarded as being characteristic of a site or group of sites when their indicator value reached a significant maximum > 70% (van Rensburg *et al.* 1999).

Because tourist species, i.e. species transient to a given assemblage, are likely both to artificially inflate estimates of species richness within habitats (Gaston *et al.* 1993), and to bias estimates of occurrence across habitats, tourist species were identified and then excluded from analyses of species ranges. Usually, tourist species are identified based on life history information (see Gaston *et al.* 1993). In the absence of such information, there is no generally accepted, quantitative method for identifying tourists based on abundance data (see Chown & Steenkamp 1996; McGeoch & Chown 1998). Nonetheless, benchmark criteria can be set to facilitate this process, and for our study we set these in the following manner. First, we assumed that a tourist species originating from an area where it achieves high abundance will be represented by more individuals than a tourist species that generally has a lower abundance in its usual habitat. We therefore considered a species a tourist to a given habitat if it was represented in that habitat by less than 5% of its total population across all habitats. This is similar to the proportion of sum criterion that Gaston (1994) suggested should be used for identifying rare species in an assemblage, although for rare species a 25% benchmark is usually used. Second, we noted that species may be rare within a given habitat, thus confounding assessments of whether it should be considered rare or a tourist species within that habitat. Thus, even if a species was considered a tourist on the grounds of the abundance criterion, it was rather regarded as rare if it occurred in more than 60% of the samples taken in the habitat for which the assessment was being made (see Dufrêne & Legendre 1997 for rationale, and McGeoch & Chown 1998 for additional discussion). Finally, species that were represented by less than five individuals in a particular habitat were regarded as tourists, regardless of the abundance criterion (such species never met the 60% sampling criterion).

2.3 RESULTS

Seventeen mite species (126 203 individuals) from 11 families were found on the shore at Macaroni Bay (Table 2.1). Three families dominated the assemblages in both abundance and diversity: the Hyadesiidae, Ameronothridae and Halacaridae. The most speciose family on the shore was the Ameronothridae, containing five species from three genera. Species richness (excluding tourists) increased from the littoral to the supralittoral, although there was a slight decrease from the lower to upper littoral zones (Table 2.1). Mite densities also showed an increase up the shore. Densities were highest in the *Mastodia* (363 890 individual.m^{-2}) and lowest in the *Caloplaca* (11 194 individuals.m^{-2}). Tourists inflated estimates of species richness considerably, although the pattern across the habitats remained similar to that found when these species were excluded (Table 2.1). The exclusion of habitats to which species were thought to be tourists resulted in fundamentally different ranges for several species (Table 2.1, Fig. 2.1).

Six insect species (1938 individuals) from three orders were found on the shore. Species richness increased from one in the littoral, to four and two species in the *Mastodia* and *Caloplaca* zones, respectively. The littoral, chironomid midge, *Telmatogeton amphibius* was the most abundant species, constituting 80% of all insects counted. In the *Mastodia*, a fly, *Apetaenus litoralis*, was numerically dominant while in the *Caloplaca* the two weevils *Bothrometopus parvulus* and *B. randi* were dominant. 97% of the insects collected (1938 individuals) were in the larval stage. Both species richness and ranges changed when tourists were excluded (Table 2.1, Fig. 2.1).

The stress value (= 0.03) for the MDS ordination indicated that a two dimensional representation of the samples was sufficient for clear interpretation of the results (Clarke 1993). Although the axes of the MDS have no units, linear distances between clusters do provide an indication of their similarity (Clarke 1993). Thus, arthropod assemblages in three of the zones, the Red, *Porphyra* and *Verrucaria* habitats (see Fig. 2.3 for a closer examination of the clustering), were more similar to each other than to those in either the *Mastodia* or *Caloplaca* zones, although the former were still significantly different from one another. The results of the Analyses of Similarity (indicated on the ordination) provided support for the groupings. There were significant differences between all the sample groups (Global-R = 0.912, $p < 0.001$), and the pairwise comparisons of the assemblages all had R values of between 0.814 and 1.000, with $p < 0.001$ (Figs 2.2 and 2.3). These results showed that the habitats defined on the basis of plant community structure differ significantly with regard to their arthropod assemblages.

TABLE 2.1 Mean densities (± SE, individuals.m^{-2}, n = 60) of the invertebrates for the five sampling habitats on Macaroni Bay. The mean total density for mites and insects was calculated by summing the number of mites and insects found in the samples. Square brackets indicate species that were regarded as tourists in a particular zone. Species richness in round brackets includes tourist species.

"Group"	Species	Red zone	*Porphyra* zone	*Verrucaria* zone	*Mastodia* zone	*Caloplaca* zone
Astigmata						
Algophagidae	*Algophagus* sp. nov. 2	0	0	0	219 ± 81	0
Hyadesiidae	*Hyadesia halophila* Fain	0	0	0	211724 ± 31743	2984 ± 1381
	H. kerguelensis Lohmann	23001 ± 4099	36684 ± 4138	85228 ± 10390	0	0
Winterschmidtiidae	*Neocalvolia* sp.	0	0	0	[11 ± 8]	1340 ± 523
Cryptostigmata						
Ameronothridae	*Alaskozetes antarcticus* (Michael)	0	0	0	4059 ± 1346	0
	Halozetes belgicae (Michael)	[6 ± 4]	[26 ± 16]	[265 ± 124]	130380 ± 25393	1817 ± 779
	H. marinus devilliersi Englebrecht	44 ± 14	[8 ± 5]	[27 ± 27]	[8 ± 5]	0
	H. marionensis Englebrecht	570 ± 139	396 ± 84	6698 ± 1009	3841 ± 1244	0
	Podacarus auberti Grandjean	0	[8 ± 5]	0	12748 ± 3608	[27 ± 19]
Parakalummidae	*Porokalumma rotunda* Wallwork	0	0	0	[8 ± 5]	1777 ± 701
Mesostigmata						
Digamasellidae	*Dendrolaelaps* sp.	0	0	0	42 ± 21	199 ± 52
Rhodacaridae		0	0	[27 ± 19]	415 ± 80	0
Prostigmata						
Eupodidae	*Eupodes minutus* (Strandtman)	0	0	0	0	[66 ± 34]
Halacaridae	*Halacarellus* sp.	[12 ± 8]	[11 ± 11]	0	0	0
	Isobactrus magnus (Lohmann)	3804 ± 795	3705 ± 975	23608 ± 5766	[87 ± 25]	0
Stigmaeidae	*Eryngiopus* sp.	0	0	0	351 ± 94	2281 ± 412
Tydeidae		[3 ± 3]	0	0	0	703 ± 148
Total mite density		**27439 ± 4510**	**40838 ± 4235**	**115852 ± 14975**	**363890 ± 57200**	**11194 ± 2439**
Coleoptera	*Bothrometopus parvulus* (Waterhouse)	0	0	0	98 ± 28	531 ± 96
	B. randi (Jeannel)	0	0	[13 ± 13]	[8 ± 5]	106 ± 55
	Palirhoeus eatoni (Waterhouse)	0	0	0	200 ± 53	[13 ± 13]
Diptera	*Apetaenus litoralis* (Eaton)	0	0	0	864 ± 197	[40 ± 23]
	Telmatogeton amphibius (Eaton)	3868 ± 876	860 ± 141	[119 ± 96]	0	0
Hymenoptera	*Kleidotoma icarus* (Quinlan)	0	0	0	79 ± 25	0
Total insect density		**3868 ± 876**	**860 ± 141**	**133 ± 97**	**1249 ± 216**	**690 ± 119**
Oligochaete		875 ± 327	[4 ± 4]	0	0	0
Species richness	**Acari**	**4 (7)**	**3 (7)**	**3 (6)**	**9 (13)**	**7 (9)**
	Insects	**1 (1)**	**1 (1)**	**0 (2)**	**4 (5)**	**2 (4)**

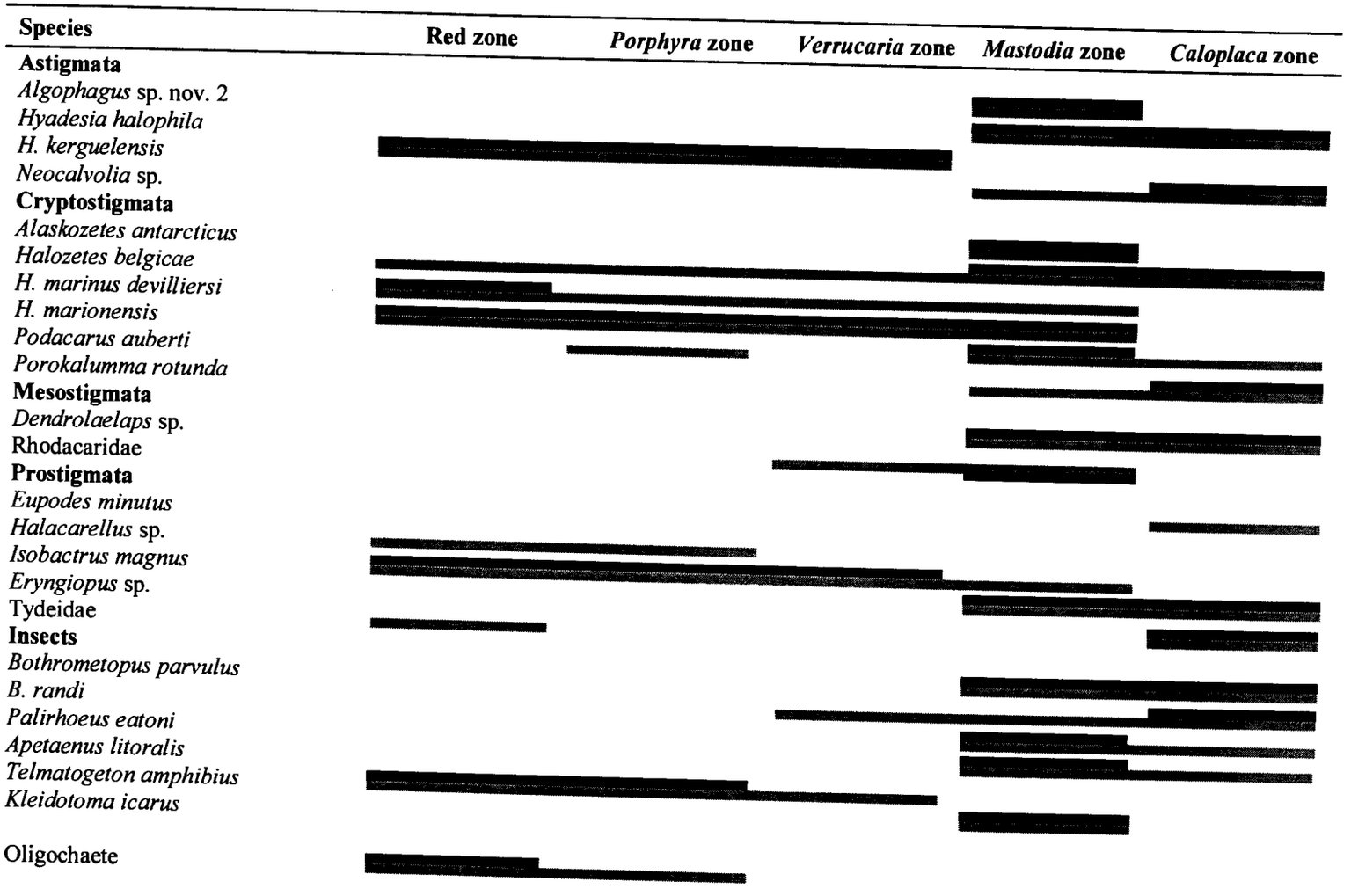

FIG. 2.1 Diagrammatic representation of species ranges on the shore at Macaroni Bay. Black bars indicate distributions excluding habitats where a species was considered a tourist (see square brackets in Table 1) and grey bars indicate distributions including these habitats.

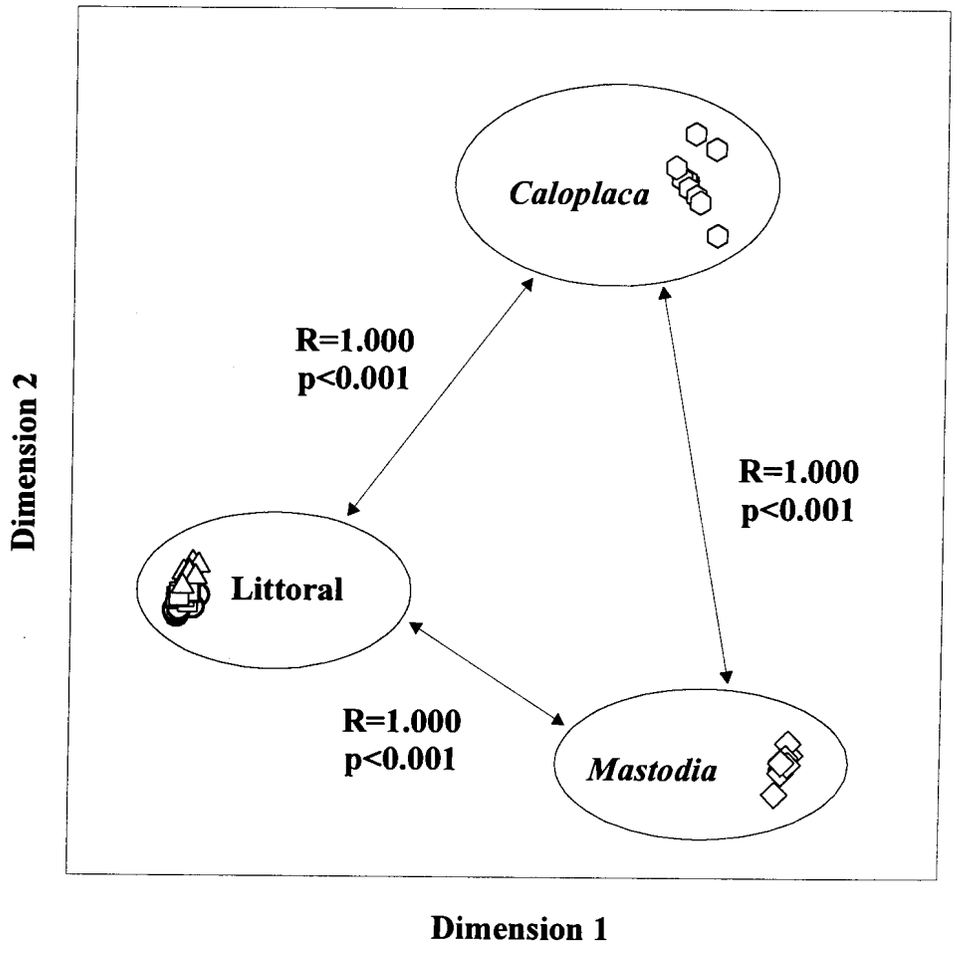

FIG. 2.2 Multi-dimensional scaling ordination of species abundance in the invertebrate assemblages of the five sampled zones. The scale of the ordination prevents the three lower habitats from being seen and these have been grouped together as "littoral" (shown in Fig. 2.3). The distances between points on the ordination are relative measures of their similarity and tested with R. If R is significantly different from zero, then there are significant differences between assemblages. Stress = 0.03

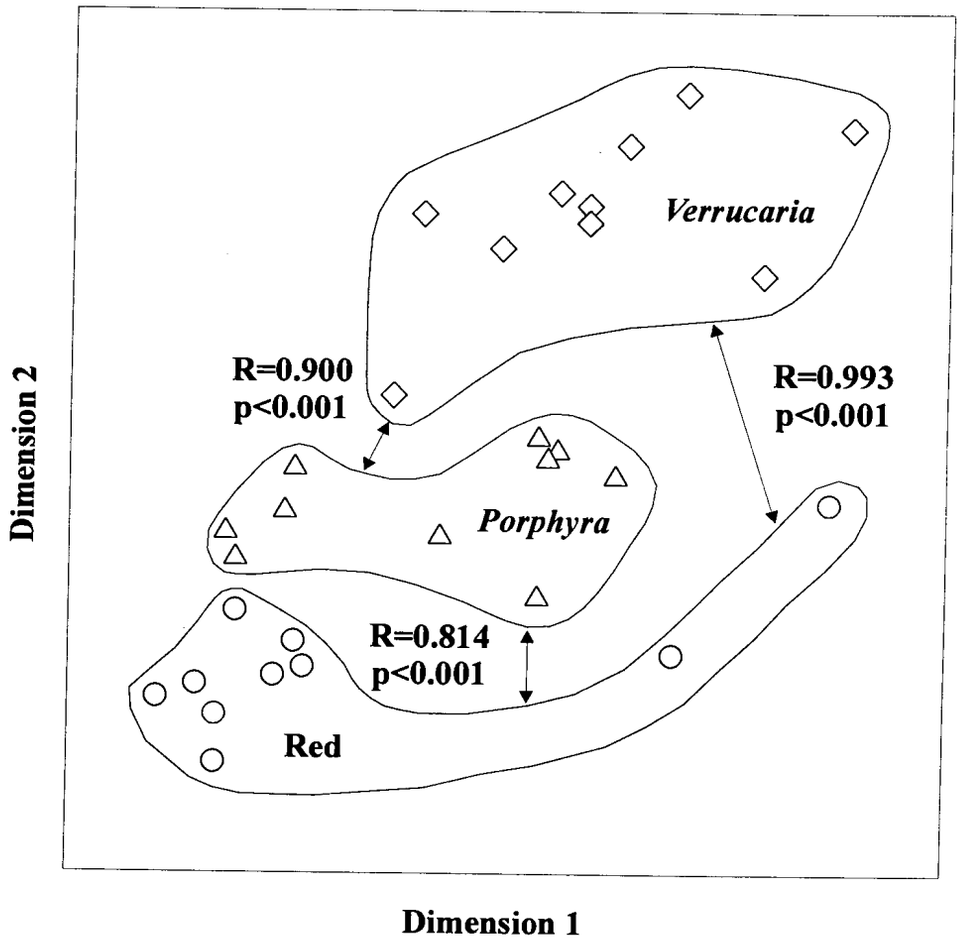

FIG. 2.3 Multi-dimensional scaling ordination of species abundance in the invertebrate assemblages of the three lower zones. The distances between points on the ordination are relative measures of their similarity and these are tested using the R-value. If R is significantly different from zero, then there are significant differences between assemblages. Stress = 0.03

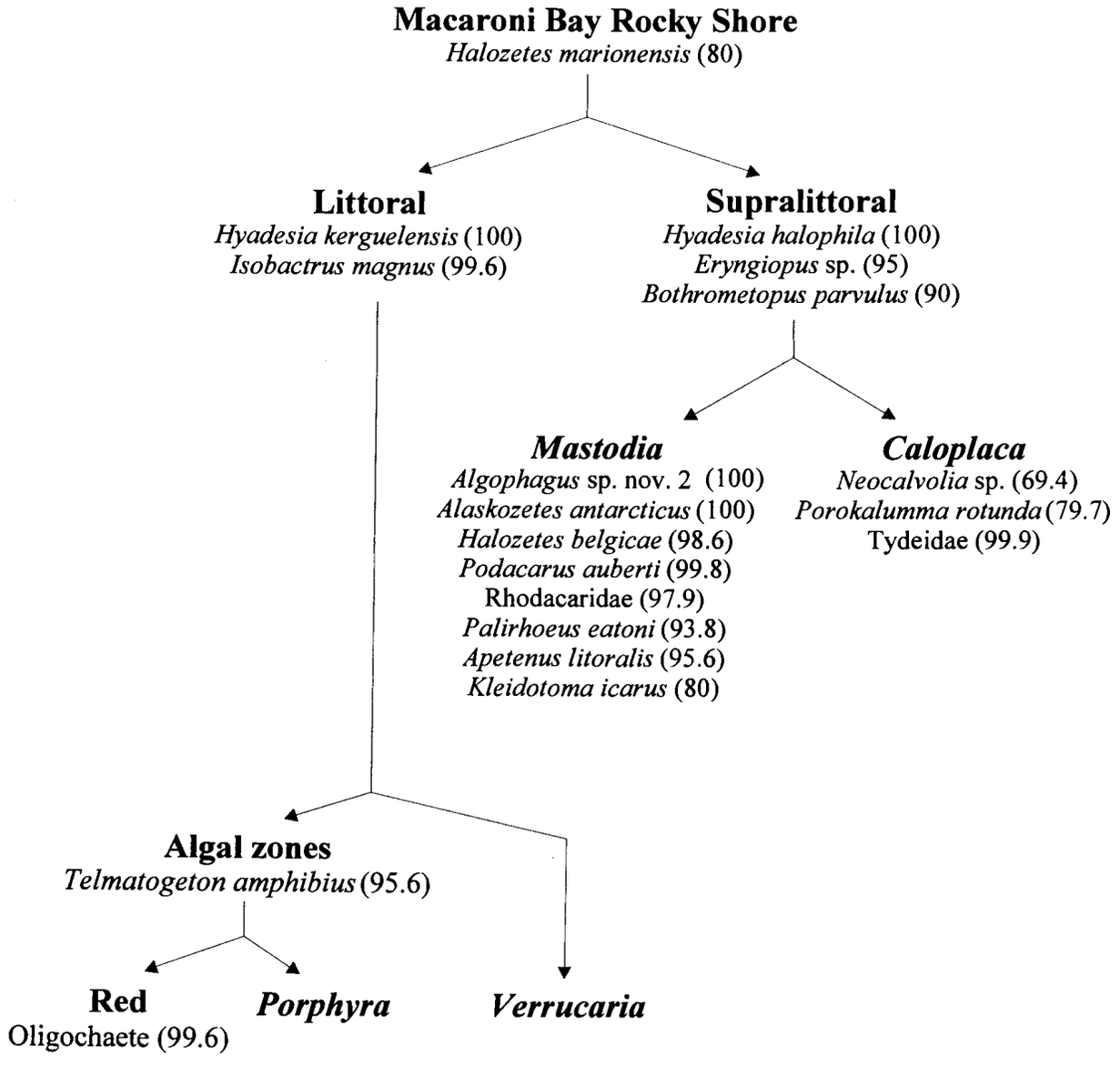

FIG. 2.4 The shoreline habitats on Marion Island with the species characteristic of each of these habitats (zones) or groups of zones indicated. For each species the significant ($p < 0.05$) indicator value (%) is shown in parentheses.

The IndVal analyses indicated that *Halozetes marionensis* is a generalist species occurring in all of the zones (Fig. 2.4). Although its indicator value was not significant, significance at this level of the hierarchy cannot be determined because of the nature of the permutation procedure used to calculate significance (Dufrêne & Legendre 1997). The first split in the hierarchy divided the sampling groups into littoral and supralittoral habitats (Fig. 2.4). The littoral sites were characterised by *Hyadesia kerguelensis* and *Isobactrus magnus*, while the supralittoral was characterised by *Hyadesia halophila*, *Eryngiopus* sp. and *Bothrometopus parvulus*. The Acari for the littoral habitats were eurytopic with no mite indicators for any of the lower clustering levels. *Telmatogeton amphibius*, divided the algae from the lichen-dominated littoral sites, and the presence of an oligochaete species (the only non-arthropod consistently recorded in the samples) separated the Red from the *Porphyra* zone.

The two supralittoral sites both had a number of characteristic, and thus habitat-specific species (Fig. 2.4). Five mite and three insect species were characteristic of the *Mastodia* sites. Although *Algophagus* sp. appeared to be characteristic of the *Mastodia* zone it was present only in samples collected in June 1997 (55 individuals) and April 1998 (three individuals). *Algophagus* sp. occurs at high densities in the supralittoral pools and it is probable that these *Mastodia* samples were collected close to the edge of one of the pools. However, this was not the case for *Alaskozetes antarcticus*, *Halozetes belgicae*, *Palirhoeus eatoni*, *Apetaenus litoralis* and *Kleidotoma icarus* which are restricted to this zone. Three species, *Neocalvolia* sp., *Porokalumma rotunda* and Tydeidae, were characteristic of the *Caloplaca* zone.

2.4 Discussion

2.4.1 Shoreline arthropod communities in the sub-Antarctic

Based on their arthropod assemblages, five distinct habitats were identified on the rocky shore at Macaroni Bay. These three littoral and two supralittoral zones correspond to and support the cryptogam-based zonation patterns described by de Villiers (1976), and are indicative of habitat selection by the Acari and insects (see below). Similar patterns of acarine zonation have been recorded from rocky shores elsewhere (e.g. Pugh & King 1985a, 1985b, 1988; Luxton 1990a, 1990b). In the sub-Antarctic, Bellido (1981) examined the shores on Kerguelen and recorded similar acarine densities to those found on Marion Island, with densities of between 7 220 and 128 100 individuals.m^{-2} for the mid-littoral, i.e. *Porphyra* and *Verrucaria* habitats, respectively, and 9700 to 32 900 individuals.m^{-2} for the supralittoral zones, i.e. *Caloplaca* and *Verrucaria*, respectively. In Bellido's (1981) study, the most abundant family found was the Ameronothridae, with four species (*Alaskozetes antarcticus*, *Halozetes belgicae*, *H. intermedius* and *H. marinus*) showing distinct vertical zonation. *A. antarcticus* and *H. belgicae*, together with

Porokalumma rotunda (Parakalummidae) were found in the supralittoral, while *H. intermedius* dominated the *Verrucaria* zone, and *H. marinus* occurred predominantly in patches of algae. This zonation pattern is almost identical to that found for the ameronothrids studied here, except that on Marion Island *H. intermedius* is absent and is replaced by *H. marionensis*. Although *Podacarus auberti*, the fifth ameronothrid species found at Macaroni Bay, was absent from the shore on Kerguelen it was found in the adjacent halophytic vegetation. This is most likely due to the absence of a broad *Mastodia* zone on the latter island.

Broadly similar zonation patterns to those found in this study were also recorded from South Georgia (Pugh & Bartsch 1993; Pugh & MacAlister 1994; Pugh 1995). For example, on South Georgia, *Hyadesia halophila* is restricted to the upper littoral (Pugh 1995), while on Marion Island this species occurs predominantly in the supralittoral. With regard to the ameronothrids, only two *Halozetes* species, *H. littoralis* and *H. marinus*, occur in the littoral on South Georgia. In the supralittoral, Pugh and MacAlister (1994) found two additional ameronothrid species, *Alaskozetes antarcticus* and *Halozetes belgicae*, bringing the total number of species in this family up to four. Thus, the ameronothrids show similar species richness and patterns of zonation on South Georgia, Kerguelen and Marion Islands. Despite these similarities, the vertical ranges of the South Georgian species do appear to be much broader than those recorded for Marion Island (compare Table 1 here with Pugh & MacAlister 1994; Pugh 1995). We suspect that these differences may be a consequence of the inclusion of tourist species into the South Georgian samples.

2.4.2 Tourist species

A tourist can be defined as a species of which the individuals have no intimate or lasting association with the assemblage in which they are found (Gaston *et al.* 1993; Chown & Steenkamp 1996). In consequence, these species do not contribute significantly to the food web constituted by that assemblage. On rocky shores, where distinct arthropod assemblages are found adjacent to each other, tourists can be common as a result of local dispersal agents (e.g. wind, waves and other animals) or because mobile species may wander into adjacent zones. The importance of identifying such tourists is most evident when habitat specificity or the extent of species ranges across the shore are being assessed. In these cases, the use of qualitative data may lead to partially erroneous conclusions because tourist species are not excluded. On the other hand, quantitative data allow this to be done, and the resulting differences in species ranges can be marked (Fig. 2.1). For example, *Halozetes marinus*, was found in significant densities only in the lower littoral, although a few isolated specimens were recorded from the higher zones. If the distributional range of this species across the shore was described solely on the basis of its presence

within a habitat, then it would be considered widespread, occurring across four zones (from the Red to the *Mastodia* zones). Thus what is in fact a stenotopic species would erroneously be described as eurytopic. Clearly, similar, mistaken assessments could be made for other species on the Macaroni Bay shore. Therefore, it seems likely that qualitative studies of shore zonation patterns on other sub-Antarctic islands have overestimated the ranges of many of the species examined.

Likewise, when arthropod species richness of the zones at Macaroni Bay was calculated using species presence-absence data, without taking abundance into account, the estimates were inflated. Thus, the presence of tourist species resulted in an increase in species richness in each shore zone of between 30 - 100% and 0 - 200%, for the mites and insects, respectively. Other studies have shown similar increases in species richness when tourists are included (e.g. Pimentel & Wheeler 1973; Gaston *et al.* 1993; Chown & Steenkamp 1996), with profound consequences for assessments of community structure and their underlying processes (see Gaston *et al.* 1993; Chown & Steenkamp 1996 for further discussion). There is, therefore, clearly scope for an extension of the kinds of quantitative sampling we have undertaken here to other islands.

Even with tourist species excluded, patterns in arthropod species richness across the shore on Marion Island were nonetheless similar to those found elsewhere. For example, in the United Kingdom, diversity of the 'terrestrial' Acari (*sensu* Pugh & King 1985a) has been shown to increase up the shore from the littoral to the supralittoral (Pugh & King 1985a). On Marion Island, mite species richness increases from three non-halacarid species in the littoral to nine species in the *Mastodia* and seven species in the *Caloplaca* zones. Changes in acarine diversity across the shore are generally related to changes in lichen morphology (Pugh & King 1988), and this would explain the differences in species richness between the lichen zones at Macaroni Bay. The foliose lichen, *Mastodia*, provides more shelter and probably accumulates more wind-blown detritus and guano than does the crustose *Caloplaca*. The distribution of *Podacarus auberti*, one of the largest mite species on Marion Island, lends support to this idea. This species is found in the *Mastodia* zone and in the vegetation adjacent to the shore, but it does not occur in the intervening *Caloplaca* zone. The flat encrusting *Verrucaria* sp. also provides almost no shelter for arthropods, and in consequence species richness is much reduced in this zone.

Similar patterns were shown by the insects, with an increase from the littoral, where only one species was present, to the supralittoral zones where two to four species occurred. Species richness, and density also differed markedly between the two supralittoral habitats, and once again this can be ascribed to differences in lichen morphology. For example, in patches where the *Caloplaca* has separated from the rock, detritus accumulates and these areas are favoured by the larvae of *Bothrometopus parvulus*, the most eurytopic curculionid on Marion Island (Chown 1989, 1992). On the other hand, virtually no insects

are found in the flat patches of *Caloplaca* that are still firmly attached to the rock substratum, creating an uneven distribution of species within the zone.

2.4.3 Habitat specificity

With regard to habitat specificity, the shore was characterised by one extremely eurytopic species, *Halozetes marionensis*, which was found in all zones with the exception of the *Caloplaca*. In this study, *Hyadesia kerguelensis* and *Isobactrus magnus* were found throughout the littoral and these genera show similar eurytopic patterns on other sub-Antarctic islands (Pugh 1993; Pugh & Bartsch 1993), and on British shores (Pugh & King 1985b). Both *Halozetes marinus* and *Halacarellus* sp. were poorly represented in our samples, and we considered the former a rare species on this shore, and the latter a tourist species. *H. marinus* was found to be more abundant in thick mats of filamentous algae on sheltered shores (Pugh 1996; personal observation) supporting the idea that it is rare on wave exposed shores. Despite the low abundances of these species, it was nonetheless clear that they are amongst the most stenotopic species in the littoral and this is true of these species on other sub-Antarctic islands (Pugh & Bartsch 1993; Pugh 1995). The only other stenotopic species found in the littoral zone was *Telmatogeton amphibius*, a flightless chironomid midge restricted to the algal zones. The specificity of this marine midge to the lower littoral is well known both on Marion Island (Crafford *et al.* 1986) and elsewhere (e.g. Dreux & Voisin 1992), and seems to be characteristic of this genus (Sublette & Wirth 1980).

The supralittoral at Macaroni Bay represents an interface between the littoral and terrestrial environments (see Pugh & MacAlister 1994 for support of this idea on South Georgia). At Macaroni Bay, 50% of the Acari and 33% of the insect species were shared between the supralittoral and terrestrial habitats, with only one species shared with the littoral assemblage (see Crafford *et al.* 1986 and Marshall *et al.* 1999 for data on insect and mite distributions on Marion Island, respectively). Of the three species occurring throughout the supralittoral (see Fig. 2.4), *Hyadesia halophila* is restricted to this broad zone on both Marion and on other sub-Antarctic islands (Pugh 1993), and the genus is unique to coastlines (Pugh & MacAlister 1994). On the other hand, the *Eryngiopus* sp. and *Bothrometopus parvulus*, have been recorded from other epilithic habitats on the island (Crafford *et al.* 1986; Chown 1989; Marshall *et al.* 1999). The epilithic fellfield habitat is similar to the supralittoral in terms of its structure and lack of vascular vegetation (Gremmen 1981) and this may account for the presence of these species throughout this biotope.

The indicator value analysis suggested that eight arthropod species are specific to the lower supralittoral, or *Mastodia* zone. Two of these species (or more correctly, taxa) are widespread elsewhere in terrestrial habitats. *Podacarus auberti* has been recorded from a variety of terrestrial vegetation types

on Marion Island (Marshall *et al.* 1999), whereas taxonomic resolution within the Rhodacaridae, which are found in all habitats on Marion Island, is insufficient to determine whether the species on the shore is specific to this zone. Of the remaining six species, *Algophagus* sp., *Alaskozetes antarcticus*, *Palirhoeus eatoni*, *Apetaenus litoralis* and *Kleidotoma icarus* were unique to the *Mastodia* zone, while *Halozetes belgicae* reached extremely high densities in this zone, but was also found in lower abundances in the *Caloplaca* zone. This latter circumpolar mite species is found in a broad range of habitats elsewhere in the sub-Antarctic. It has been collected from supralittoral lichens on South Georgia (Pugh & MacAlister 1994) and Kerguelen (Bellido 1981) and *Azorella selago* cushions on Heard Island (Starý *et al.* 1997). Pugh (1993) notes that it has been recorded from mosses, lichens, algae and rocks in the littoral and supralittoral zones and from inland habitats across the Antarctic region. However, on Marion Island it is restricted to the supralittoral and found mostly amongst *Mastodia* thalli. The reason for the reduced range on Marion is probably due to the presence of *Halozetes fulvus*. The endemic *H. fulvus* occurs in all terrestrial habitats on Marion Island with the exception of the supralittoral (Marshall *et al.* 1999). It is also similar in size and physiology to *H. belgicae* (unpublished data). These facts strongly suggest that competitive exclusion has constrained the distributional range of *H. belgicae* on Marion Island, although at present there is only circumstantial evidence for this idea.

The habitat specificity found for the insects in the *Mastodia* zone is not entirely surprising (see Crafford *et al.* 1986; Chown 1989), although our study provides the first quantitative evidence in support of this specificity. For example, Chown (1993b) suggested that *Palirhoeus eatoni* might be restricted to *Prasiola* (or its lichenized form *Mastodia*) in the Macaroni Bay area, although he provided no quantitative data in support of this idea.

Only a single species, *Porokalumma rotunda*, was unique to the *Caloplaca* zone, despite the fact that both *Neocalvolia* sp. and Tydeidae also appeared to be restricted to this zone. However, the genus *Neocalvolia* was restricted to salt-spray communities (e.g. *Cotula plumosa* and *Crassula moschata*) and was an excellent indicator for coastal areas (Barendse 2000), while the Tydeidae are widespread across the island, although here too future taxonomic resolution within the family on the island might indicate that one or a few species are specific to this zone.

Thus, as far as habitat specificity in the arthropods is concerned, the shore was characterised both by eurytopic and stenotopic species. Although the presence of some generalist species is in keeping with claims for the predominance of generalists in the sub-Antarctic (e.g. Crafford *et al.* 1986; Crafford 1990), the occurrence of at least eight habitat specific species is notable. It supports the idea that habitat specificity may be more well- developed in the older epilithic habitats, than in the younger vegetated ones (see Chown 1990; 1994), as a result of the longer time available for colonisation of the epilithic biotope and hence the development of interspecific interactions within it (see Arthur 1987 for discussion, and

Davies 1987; Chown 1992 for evidence for insects). Nonetheless, there have been no formal demonstrations of interspecific interactions between the Acari on Marion Island.

In sum, we have shown that patterns in arthropod diversity across the shore on Marion Island are similar to those recorded both in the sub-Antarctic and elsewhere, and that habitat specificity is not uncommon in shoreline arthropods. By undertaking a quantitative analysis we were also able to characterise more accurately species ranges across the shore, and habitat specificity for each of the zones. The pronounced differences in both the species richness patterns and the ranges identified for each species when tourists were excluded compared to an analysis including all species suggests that such quantitative surveys could be usefully applied to shoreline arthropod assemblages across the sub-Antarctic. Only once this has been done, will meaningful comparisons of the structure and functioning of these assemblages on islands that differ markedly in age, glacial history, and species richness (see Chown *et al.* 1998) be possible.

2.5 REFERENCES

Arthur, W. (1987) The niche in competition and evolution. Wiley, New York

Barendse, J. (2000) *Patterns in the distribution and abundance of terrestrial arthropods on sub-Antarctic Marion Island*. MSc Thesis, University of Pretoria

Bellido A. (1981) Les biocenoses du littoral rocheux aux Iles Kerguelen. *C.N.F.R.A.* 51:81-92

Blankley, W.O. & Grindley, J.R. (1985) The intertidal and shallow subtidal food web at Marion Island. In: Siegfried, W.R., Condy, P.R. & Laws, R.M. (eds) *Antarctic nutrient cycles and food webs*. Springer-Verlag, Berlin, pp 630-636

Chown, S.L. (1989) Habitat use and diet of Ectemnorhinini. *Antarctic Science* 1:23-30

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

Chown, S.L. (1992) A preliminary analysis of weevil assemblages in the Sub-Antarctic: local and regional patterns. *Journal of Biogeography* 19:87-98

Chown, S.L. (1993a) Desiccation resistance in six sub-Antarctic weevils (Coleoptera: Curculionidae): humidity as an abiotic factor influencing assemblage structure. *Functional Ecology* 7:318-325

Chown, S.L. (1993b) Instar number and mass of *Palirhoeus eatoni* (C.O. Waterhouse) and *Bothrometopus randi* Jeannel (Coleoptera: Curculionidae) from Subantarctic Marion Island. *Coleopterists Bulletin* 47:69-73

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

Chown, S.L., Gremmen, N.J.M. & Gaston, K.J. (1998) Ecological biogeography of Southern Ocean islands: species-area relationships, human impacts and conservation. *American Naturalist* 152:562-575

Chown, S.L. & Steenkamp, H.E. (1996) Body size and abundance in a dung beetle assemblage: optimal mass and the role of transients. *African Entomology* 4:203-212

Chown, S.L., van der Merwe, M. & Smith, V.R. (1997) The influence of habitat and altitude on oxygen uptake in sub-Antarctic weevils. *Physiological Zoology* 70:116-124

Chown, S.L. & van Drimmelen, M. (1992) Water balance and osmoregulation in weevil larvae (Coleoptera: Curculionidae: Brachycerinae) from three different habitats on sub-Antarctic Marion Island. *Polar Biology* 12:527-532

Clarke, K.R. (1993) Non-parametric multivariate analysis of changes in community structure. *Australian Journal of Ecology* 18:117-143

Clarke, K.R. & Warwick, R.M. (1994) *Change in marine communities: an approach to statistical analysis and interpretation*. Natural Environment Research Council, UK

Crafford, J.E. (1984) Life cycle and kelp consumption of *Paractora* (Diptera: Helcomyzidae): a primary decomposer of stranded kelp on Marion Island. *South African Journal of Antarctic Research* 14:18-22

Crafford, J.E. (1990) The role of feral house mice in ecosystem functioning on Marion Island. In: Kerry, K.R., Hempel, G. (eds) *Antarctic ecosystems. Ecological change and conservation. Proceedings of the 5th SCAR biology symposium*. Springer-Verlag, Berlin, pp359-364

Crafford, J.E. & Chown, S.L. (1993) Respiratory metabolism of sub-Antarctic insects from different habitats on Marion Island. *Polar Biology* 13:411-415

Crafford, J.E. & Scholtz, C.H. (1987) Phenology of stranded kelp degredation by the kelp fly *Paractora dreuxi mirabilis* (Helcomyzidae) at Marion Island. *Polar Biology* 7:289-294

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

Davenport, J., Barnett, P.R.O. & McAllen, R.J. (1997) Environmental tolerances of three species of the harpacticoid copepod genus *Tigriopus*. *Journal of Experimental Marine Biology and Ecology* 77:3-16

Davenport, J. & MacAlister, H. (1996) Environmental conditions and physiological tolerance of intertidal fauna in relation to shore zonation at Husvik, South Georgia. *Journal of the Marine Biological Association of the United Kingdom* 76:985-1002

Davenport, J. & Stevenson, T.D.I. (1998) Intertidal colonization rates. A matched latitude, north v. south, remote v. near shore island experiment. *Diversity and Distributions* 4:87-92

Davies, L. (1987) Long adult life, low reproduction and competition in two sub-Antarctic carabid beetles. *Ecological Entomology* 12:149-162

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

Dreux, P. & Voisin, J.F. (1992) Faune entomologique de l'île des Pingouins (archipel Crozet). *Bulletin de la Société entomologique de France* 97:453-464.

Dufrêne, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible assymmetrical approach. *Ecological Monographs* 67:345-366

Engelbrecht, C.M. (1974) The genus *Halozetes* (Oribatei: Acari) on Marion Island. Navorsinge van die Nasionale Museum 3:1-25

Fuller, N.R. (1967) A preliminary report on the littoral ecology of Marion and Prince Edward Islands. *South African Journal of Science* 63:248-252

Gaston, K.J. (1994) *Rarity*. Chapman & Hall, London

Gaston, K.J., Blackburn, T.M., Hammond, P.M. & Stork, N.E. (1993) Relationships between abundance and body size: where do tourists fit? *Ecological Entomology* 18:310-314

Gremmen, N.J.M. (1981) *The vegetation of the Subantarctic islands Marion and Prince Edward*. Dr W. Junk, The Hague

Knox, G.A. (1994) *The biology of the Southern Ocean*. Cambridge University Press, Cambridge

Kronberg, I. (1988) Structure and adaptation of the fauna in the black zone (littoral fringe) along rocky shores in northern Europe. *Marine Ecology Progress Series* 49:95-106

Lewis, J.R. (1964) *The ecology of rocky shores*. The English Universities Press, London

Lively, C.M., Raimondi, P.T. & Delph, L.F. (1993) Intertidal community structure: space-time interactions in the Northern Gulf of California. *Ecology* 74:162-173

Luxton, M. (1990a) The marine littoral mites of the New Zealand region. *Journal of the Royal Society of New Zealand* 20:367-418

Luxton, M. (1990b) Local distribution and habitat of mites (Acari) on the sea coast of New Zealand. *Journal of the Royal Society of New Zealand* 20:419-426

Marshall, D.J., Gremmen, N.J.M., Coetzee, L., O'Connor, B.M., Pugh, P.J.A., Theron, P.D. & Ueckermann, E.A. (1999) New records of Acari from the sub-Antarctic Prince Edward Islands. *Polar Biology* 21:84-89

Mathieson, A.C. & Nienhuis, P.H. (1990) *Ecosystems of the world 24 - Intertidal and littoral ecosystems*. Elsevier, Amsterdam

McGeoch, M.A. & Chown, S.L. (1998) Scaling up the value of bioindicators. *Trends in Ecology and Evolution* 13:46-47

Pimentel, D. & Wheeler, A.G. (1973) Species and diversity of arthropods in the alfalfa community. *Environmental Entomology* 2:659-668

Pugh, P.J.A. (1993) A synonymic catalogue of the Acari from Antarctica, the sub-Antarctic islands and the Southern Ocean. *Journal of Natural History* 27:323-421

Pugh, P.J.A. (1995) Air-breathing littoral mites of sub-Antarctic South Georgia. *Journal of Zoology, London* 236:649-666

Pugh, P.J.A. (1996) Using artificial substrata to monitor how cryptofaunal Acari colonize littoral algae on sub-Antarctic South Georgia. *Acarologia* 37:189-200

Pugh, P.J.A. & Bartsch, I. (1993) Ecology of the littoral Halacaridae (Acari: Prostigmata) of South Georgia in the sub-Antarctic. *Journal of Natural History* 28:75-85

Pugh, P.J.A. & Davenport, J. (1997) Colonisation vs. disturbance: the effects of sustained ice-scouring on intertidal communities. *Journal of Experimental Marine Biology and Ecology* 210:1-21

Pugh, P.J.A. & King, P.E. (1985a) The vertical distribution of the British intertidal Acari - the non halacarid fauna (Arachnida: Acari). *Journal of Zoology, London* 207:21-33

Pugh, P.J.A. & King, P.E. (1985b) Vertical distribution and substrate association of the British Halacaridae. *Journal of Natural History* 19:961-968

Pugh, P.J.A. & King, P.E. (1988) Acari of the British supralittoral. *Journal of Natural History* 22:107-122

Pugh, P.J.A. & MacAlister, H.E. (1994) Acari of the supralittoral zone on sub-Antarctic South Georgia. *Pedobiologia* 38:552-565

Ricketts, E.F. & Calvin, J. (1968) *Between Pacific Tides*. 4th Edition. Standford University Press, Stanford, California

Simpson, R.D., Smith, S.D.A. & Pople, A.R. (1995) The effects of a spillage of diesel fuel on a rocky shore in the sub-Antarctic region (Macquarie Island). *Marine Pollution Bulletin* 31:367-371

Smith, J.M.B. & Simpson, R.D. (1985) Biotic zonation on rocky shores of Heard Island. *Polar Biology* 4:89-94

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

Sømme, L. & Block, W. (1984) Ecophysiology of two intertidal mites at South Georgia. *Oikos* 42:276-282

Starý, J., Block, W. & Greenslade, P. (1997) Oribatid mites (Acari: Oribatida) of sub-Antarctic Heard Island. *Journal of Natural History* 31:545-553

Stephenson, T.A. & Stephenson, A. (1972) *Life between tidemarks on rocky shores*. W.H. Freeman and Company, San Francisco

Sublette, J.E. & Wirth, W.W. (1980) The Chironomidae and Ceratopogonidae of New Zealand's subantarctic islands. *New Zealand Journal of Zoology* 7:299-378.

Travé, J. (1981) Les biocénoses halophiles d'Acariens de l'archipel de Kerguelen. *C.N.F.R.A.* 48:149-158

Travé, J. (1982) Structure des peuplements de micro-arthropodes à Kerguelen. Essai de Synthèse. *C.N.F.R.A.* 51:73-80

Underwood, A.J. (1996) Detection, interpretation, prediction and management of environmental disturbances: some roles for experimental marine ecology. *Journal of Experimental Marine Biology and Ecology* 200:1-27

Underwood, A.J. & Chapman, M.G. (1996) Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia* 107:212-224

Usher, M.B., Booth, R.G. & Sparkes, K.E. (1982) A review of progress in understanding the organization of communities of soil arthropods. *Pedobiologia* 23:126-144

van der Merve, M., Chown, S.L. & Smith, V.R. (1997) Thermal Tolerance Limits in six weevil species (Coleoptera, Curculionidae) from sub-Antarctic Marion Island. *Polar Biology* 18:331-336

van Rensburg, B.J., McGeoch, M.A., Chown, S.L. & van Jaarsveld, A.S. (1999) Conservation of heterogeneity among dung beetles in the Maputaland centre of endemism, South Africa. *Biological Conservation* 88:145-153

CHAPTER 3 PATTERNS OF AGGREGATION AND COVARIATION IN LITTORAL ARTHROPOD ASSEMBLAGES

3.1 INTRODUCTION

It is widely accepted that many different processes, often operating in opposing directions, influence community structure. Direct positive (e.g. habitat amelioration and mutualisms, Bertness & Callaway 1994; Bertness & Hacker 1994; Bertness & Leonard 1997) and negative interactions (e.g. disturbance and competition, Begon *et al.* 1990), as well as indirect effects (see Strauss 1991; Wootton 1993; Menge 1995) have all been shown to have varying levels of importance in the structuring of communities. How the relative contribution of these processes change across environmental gradients is of particular interest. For example, in rocky intertidal habitats that occur across steep environmental gradients (Bertness & Leonard 1997), the physio-chemical stresses that organisms experience at different levels are well documented (see Lewis 1964; Stephenson & Stephenson 1972; Mathieson & Nienhuis 1990) and consequently processes structuring the communities differ in their importance across the gradient (see Russel 1990; Dudgeon *et al.* 1999). Knowing whether vertical or horizontal biotic interactions predominate, relative to constraints posed by abiotic conditions, can provide considerable insight into the processes structuring the communities along the gradient. For organisms of marine origin, competition sets limits to their lower distribution boundary, while the upper boundary is determined by ecophysiological tolerances to environmental extremes (Hay 1981; Hawkins & Hartnoll 1985; Davenport & MacAlister 1996). The reverse is apparently true for terrestrial organisms living in littoral communities, where the lower limit to their distributions is set by physiochemical tolerances and the upper limits by competition (e.g. salt marsh perennials - Bertness 1991). This pattern has been proposed to hold for terrestrial mite species living on shores (Pugh & King 1985a; Pugh 1995) where the lower limit of a species range is thought to be set by tolerance to abiotic factors such as salinity, substrate moisture content, inundation time vs. foraging time and dislodgement (Pugh & King 1985a; Luxton 1990). In contrast the upper distributional limits are thought to be determined at least partially by competitive interactions (Pugh 1995). To date there are no studies which have sought to test this hypothesis.

If competition occurs between ecologically similar species that share resources, and they are found to coexist then there must be some process which facilitates their coexistence. For example, coexistence can be maintained through species traits (e.g. resource partitioning) or ecological processes (e.g. physio-chemical stress or disturbance) that reduce or prevent competition (Dudgeon *et al.* 1999). The aggregation model of coexistence is one model that allows for species with similar ecological requirements to coexist.

The model was developed to explain the coexistence of heterospecifics in ephemeral habitats (Atkinson & Shorrocks 1984) and since then there have been numerous experimental studies, across a range of taxa, supporting it (e.g. carrion flies - Hanski 1987; Ives 1991; Kouki & Hanski 1995; fruitflies - Shorrocks *et al.* 1990; Sevenster & van Alphen 1996; Inouye 1999; Toda *et al.* 1999; dung beetles - Giller & Doube 1994; also see Rosewell *et al.* 1990). The aggregation model predicts that intraspecific aggregation over habitat patches stabilises the coexistence of species by reducing interspecific competition, allowing inferior competitors to persist in the environment (see Ives 1988; Sevenster 1996; Inouye 1999). The aggregation mechanism does not require that competitors differ in their ability to find or colonise patches, nor their ability to detect the presence or absence of other individuals (Inouye 1999). Instead, it assumes that species are independently distributed among patches. The process thus ignores details of adult behaviour that are responsible for the spatial patterns, but concentrates on the consequences of the aggregation regardless of its origin (Inouye 1999).

Mercer *et al.* (in preparation) have shown that the rocky shore arthropods on Marion Island are habitat specific, exhibiting distinct zonation patterns. This paper assesses species interactions occurring within and across the five zones on the shore at Macaroni Bay, testing the hypothesis that species interactions have a stronger influence on the structure of arthropod assemblages in the supralittoral than in the littoral habitats. Levels of intraspecific and interspecific aggregation were used to test for the possibility of coexistence between species.

3.2 METHODS

Fieldwork was carried out between May 1997 and May 1998 at Macaroni Bay (GPS location: 46°53'26.9"S, 37°52'33.0"E) on Marion Island. The northern section of Macaroni Bay has a sloping, unbroken rocky shore which displays zonation patterns typical of Marion Island (de Villiers 1976). The zonation is also similar to the general pattern found in Antarctic shoreline communities (Knox 1994). Based on the presence/absence of selected cryptogram species and de Villiers' (1976) criteria, five zones, three littoral and two supralittoral, were identified on the shore (Fig. 3.1). The Red zone, just above the upper limit of the kelp, *Durvillaea antarctica*, is completely covered by red algae and represents the lower littoral and the lower-most habitat sampled. The mid-shore is dominated by members of the rhodaphyte genus *Porphyra* and forms the *Porphyra* zone. The *Verrucaria* zone is the first of the lichen-dominated zones, marking the upper-shore and falling within the splash-zone. The two supralittoral zones are dominated by the lichens *Mastodia* sp. and *Caloplaca* sp. The *Caloplaca* zone is the final zone before the closed, terrestrial, vascular vegetation begins. Ten samples were collected from each of the five zones per month (June, August, October, December, February and April), with a total of 60 samples collected per

zone. Samples were collected by scraping the algae or lichen (depending on the zone) from within a circular tube down to bare rock. Sampling areas were kept constant within zones but different sampling areas (∅ between 40 mm and 85 mm) were employed between zones to accommodate for the high levels of material yielded by the different cryptogram species present.

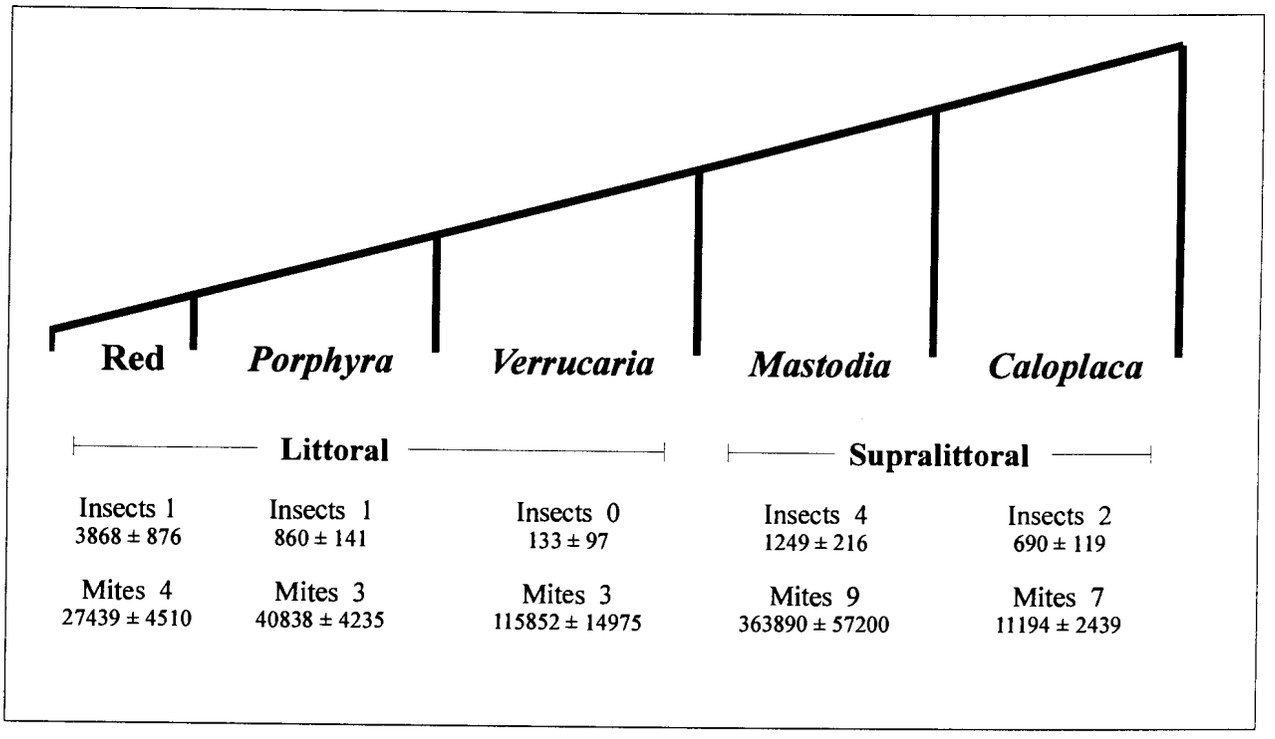

FIG. 3.1 The five zones on the shore at Macaroni Bay with insect and mite species richness and densities (ind.m^{-2} ± SE) (adapted from Mercer *et al.* in preparation). Densities include tourist species.

The samples were sorted by hand for mites and insects, which were counted and then preserved in 70% ethanol. Identification was to the lowest possible taxonomic level, mostly to genus and species (Krantz 1978, Crafford *et al.* 1986, Marshall *et al.* 1999, D.J. Marshall personal communication). However, some species were difficult to distinguish and these were combined into supra-specific taxa. These included the Rhodacaridae and Tydeidae; *Hyadesia kerguelensis* and *Hyadesia subantarctica* that were combined under *H. kerguelensis*, and *Rhombognathus auster*, if present, which was counted as *Isobactrus magnus*.

Generic and familial feeding biologies were obtained from the literature (see Gressitt & Shoup 1967; Strong 1967; Pugh & King 1985b; Crafford *et al.* 1986; Pugh & King 1988; Luxton 1990) and assigned to the respective taxa in this study. In consequence, there are limitations to the feeding guilds that were assigned to species in this analysis. For example, the Cryptostigmata have been described as having

highly variable diets (detritovores, fungivores, algivores, lichens, tardigrades). Nonetheless, these feeding biologies were taken to be adequate for this analysis despite the lack of taxonomic resolution.

3.2.1 Species associations and abundance covariation

Variance ratio tests were used to test for possible associations between species, and covariation between species abundances (Schluter 1984; Giller & Doube 1994; McGeoch & Chown 1997) within each of the five zones. The technique compares the observed variance in the total number of species (or individuals) in samples, with the variance expected under the null hypothesis that the occurrence or density of each species is independent of the others (Schluter 1984). The resulting variance ratio (VR) (see Appendix A) is then multiplied by the number of samples to obtain the test statistic (W) with a chi-squared distribution. If VR < 1, then there is a negative association, if VR > 1 then there is a positive association, and if VR = 1 there is no association between the species. The analysis was done firstly on all the arthropod species to see if there were any associations between species from different feeding guilds, and then on species within each of the feeding guilds to test for intraguild associations. Intraguild associations were not examined for the parasitoids because only one species was found within the guild.

3.2.2 Species aggregation

Ives' (1991) measures of intraspecific (J_x) and interspecific aggregation (C_{xy}) were used to determine the extent of positive associations within each of the five habitats. These indices are based on species abundances in samples and considered suitable since sampling areas were standardised within each zone (see Sevenster 1996 for further discussion). J and C give the percentage increase in expected numbers of conspecifics (J) and heterospecifics (C) in the sample above that expected if the species were randomly distributed (Ives 1991). In other words, $J_x = 0.75$ indicates a 75% increase in the expected number of conspecifics that occur within the same habitat unit above that expected if the individuals were randomly and independently distributed. Measures of interspecific aggregation were calculated in two ways. In the first method pairwise aggregation between all species within each habitat, C_{xy}, was determined (Ives 1991). In the second method aggregation measures were calculated for each species, x, against the sum of all other species present in the sample (excluding x) giving a $C_{x,-x}$ measure of multispecies rather than pairwise species aggregation (after McGeoch & Chown 1997). The significance of positive intra- and interspecific aggregation measures were tested using chi-squared dispersion tests (Heath 1995) and Spearman rank correlations (Sokal and Rohlf 1995), respectively. Sequential Bonferroni techniques were employed to control for the probability of incorrectly rejecting one or more true null hypotheses (see Rice

1989). J_x, C_{xy} and $C_{x,-x}$ were not calculated for tourist species (Table 3.1) because of their low abundance (see Sevenster & van Alphen 1996), but they were included into the multispecies analyses when all species were combined (i.e. included in $-x$). Tourists are defined as species which are transient to, and which have no intimate or lasting association with the assemblage in which they are found (Gaston *et al.* 1993; Chown & Steenkamp 1996; see Mercer *et al.* in preparation for discussion on tourists in these zones).

The relative effect of spatial aggregation on coexistence was assessed by means of the relative effect of competitor aggregation, T (Sevenster 1996). In this approach the interspecific aggregation of species x and y (C_{xy}), is compared with the intraspecific aggregation of species y (J_y), to determine the effect of the aggregation on species x (Appendix A). The resultant T_{xy} is then used as a criterion for the persistence of species x in a particular habitat and ultimately as an indication of coexistence of x and y (Sevenster 1996; Sevenster & van Alphen 1996). Because interactions are likely to be asymmetrical (i.e. $T_{xy} \neq T_{yx}$) both values were calculated (see Sevenster 1996 for further discussion). T_{xy} was calculated for all pairwise associations between resident species (i.e. non-tourists, Table 3.1, see Mercer *et al.* in preparation) in each of the zones. A similar measure $T_{x,-x}$ was used to assess the effect of spatial aggregation of all other species combined, $-x$ on species x. This variation of the pairwise T_{xy} takes multispecies aggregation into consideration when assessing the effects of aggregation on species x. The significance of the component indices (i.e. C_{xy}, J_y and $C_{x,-x}$, J_{-x}) were not considered when calculating T_{xy} (and $T_{x,-x}$). The results were tested against unity (i.e. $T_{xy} < 1$ and $T_{x,-x} < 1$) using Wilcoxon sign-rank tests (WSR) and differences in the shapes of the resultant T_{xy} and $T_{x,-x}$ frequency distributions between zones were assessed using Kolmogorov-Smirnov tests (KS) (Sokal & Rohlf 1995).

3.3 Results

Seventeen mite and six insect species, representing four feeding guilds (algae, fungi & lichens, predators and parasitoids) were found on the shore (Table 3.1, Fig. 3.1, and see Mercer *et al.* in preparation for densities). The primary consumers were by far the most numerous with nine algivore and ten fungivore species. It is difficult to determine whether species cited as feeding on lichens and detritus are utilising these food items or the associated fungi. These guilds were therefore grouped together into a single fungivore feeding guild. Only three predatory species and a single parasitoid were recorded from the shore (Table 3.1).

3.3.1 Species associations and abundance covariation

The majority of the variance ratio tests were not significant and of those that were, none showed significant, negative associations (Table 3.2). When all feeding guilds were combined and species analysed together, there were positive species associations in the *Mastodia* and *Caloplaca* zones and positive abundance covariation in the *Verrucaria*, *Mastodia* and *Caloplaca* zones.

The direction of the interactions may vary with respect to a single species, depending with which other species it is interacting. For example, a species may co-vary negatively with some species (i.e. competition) and positively with others (e.g. habitat amelioration), yet an overall result of no association is discovered (Schluter 1984). For this reason I analysed the relationships between species within functional feeding guilds. Significant positive species association and abundance covariation was found for the algivore guild in the *Verrucaria* zone and positive species associations for the fungivore guild within the *Mastodia* and *Caloplaca* zones. There were no significant associations within the predator feeding guild for any of the habitats.

3.3.2 Species aggregation

Intraspecific aggregation was high within all five habitats (Table 3.3). For the majority of taxa within the five shoreline communities, the degree of aggregation, *J%*, was significantly different from zero (Table 3.3). This indicates that conspecifics were not randomly distributed within habitats but showed intraspecific aggregation. Significant interspecific, multispecies, aggregation measures, $C_{x,-x}$ which give the expected increase in heterospecifics, were not as high and ranged from 30.94% to 346.96% (Table 3.4). Pairwise, interspecific aggregations, C_{xy}, showed even fewer significant results (Table 3.5). From 331 possible pairwise interactions less than 5% were significantly different from zero (only the significant results are displayed in Table 3.5). The degree and frequency of the aggregations indicated that intraspecific interactions were generally stronger than interspecific interactions in each of the habitats and that if competition was to occur it would most likely be between conspecifics.

Relative effects of aggregation (T) were calculated and compared among the five habitats. If the quantity T_{xy} is less than unity (i.e. $T_{xy} < 1$), then the average individual of species x suffers less from species y than the average individual of y suffers from conspecifics (Sevenster & van Alphen 1996). Thus, if the inequality is met, then species x should be able to recover from low densities and persist in the presence of y (Sevenster & van Alphen 1996). If $T < 1$ then interspecific aggregation between species is greater than intraspecific aggregation. For competing species this would ultimately mean extinction, although it would not be expected to occur immediately (Sevenster & van Alphen 1996).

3.3.3 Pairwise T

T_{xy} was calculated for each pairwise combination in each of the zones and most values were below unity (Fig. 3.2 - 3.6). Median T_{xy} values were calculated for each of the zones and were all significantly less than unity (Wilcoxon sign-rank test, WSR, $p < 0.05$ for all cases, Figs 3.2 - 3.6). T_{xy} and T_{yx} (see Methods) were taken as independent observations and both were included in the analyses (see Sevenster & van Alphen 1996). These results indicate that on average intraspecific aggregation is significantly higher than interspecific aggregation within each of the five zones. Significant differences in the shape of the frequency distribution of T_{xy} were found between the Red (median $T_{xy} = 0.598$) & *Mastodia* (median $T_{xy} = 0.291$, Kolmogorov-Smirnov test, KS = 0.5231, $p < 0.001$), Red (median $T_{xy} = 0.598$) & *Caloplaca* (median $T_{xy} = 0.237$, KS = 0.5833, $p < 0.001$), *Porphyra* (median $T_{xy} = 0.480$) & *Caloplaca* (median $T_{xy} = 0.237$, KS = 0.4861, $p < 0.025$) and *Verrucaria* (median $T_{xy} = 0.501$) & *Caloplaca* (median $T_{xy} = 0.237$, KS = 0.6250, $p < 0.05$) zones. This indicates that the degree of intraspecific aggregation, relative to interspecific aggregation, is greater in the supralittoral than in the littoral habitats.

3.3.4 Multispecies T

The analysis considering all heterospecifics should provide crucial evidence for the effect of aggregation and crowding on the coexistence of species within the community as a whole (Sevenster & van Alphen 1996). If $T_{x,-x} < 1$, then the aggregation of all heterospecifics is greater than the aggregation between these species and x. In otherwords, the aggregation of all heterospecifics of x is sufficiently high to allow the persistence of x in the community. For this analysis I was only interested in the effect of whole community aggregation, $-x$, on species x and therefore only $T_{x,-x}$ and not $T_{-x,x}$ was calculated and used in the analyses. Median $T_{x,-x}$ values were significantly less than unity for the Red, *Mastodia* and *Caloplaca* zones (WSR, $p < 0.05$, see Figs 3.7, 3.10 & 3.11) but not significant for the *Porphyra* and *Verrucaria* zones (WSR, $p > 0.05$, see Figs 3.8 & 3.9). T_{xy} values were lower than those of $T_{x,-x}$ for the *Mastodia* zone (Mann-Whitney $p = 0.0003$) but were not significantly different for any of the other four zones (Mann-Whitney, $p > 0.05$). Significant differences in $T_{x,-x}$ were found between the Red (median $T_{x,-x} = 0.628$) & *Caloplaca* (median $T_{x,-x} = 0.294$, KS = 0.7778, $p < 0.05$) and *Mastodia* (median $T_{x,-x} = 0.760$) & *Caloplaca* (median $T_{x,-x} = 0.294$, KS = 0.6239, $p < 0.05$) zones.

TABLE 3.1 Species that were collected during the study and the habitats within which they were found (✓) and those to which they were tourists (×) (Mercer *et al.* in preparation).

Order / Family	Species	Habitats					Feeding Guild	Reference
		A	B	C	D	E		
Astigmata								
Algophagidae	*Algophagus* sp. nov. 2				✓		algae?	
Hyadesiidae	*Hyadesia halophila* Fain				✓	✓	algae	Pugh & King (1985b), Luxton (1990)
	H. kerguelensis Lohmann	✓	✓	✓			algae	Pugh & King (1985b), Luxton (1990)
Winterschmidtiidae	*Neocalvolia* sp.				×	✓	fungi?	
Cryptostigmata								
Ameronothridae	*Alaskozetes antarcticus* (Michael)				✓		fungi & detritus	fungivores (Pugh & King 1985b)
	Halozetes belgicae (Michael)	×	×	×	✓	✓	fungi & detritus	lichen & debris (Luxton 1990)
	H. marinus devilliersi Englebrecht	✓	×	×	×		algae	*Halozetes* spp. – lichen (Strong 1967)
	H. marionensis Englebrecht	✓	✓	✓	✓		algae	
	Podacarus auberti Grandjean		×		✓		fungi & detritus	
Parakalummidae	*Porokalumma rotunda* Wallwork				×	✓	fungi	
Mesostigmata								
Digamasellidae	*Dendrolaelaps* sp.				✓	✓	predator	Pugh & King (1988)
Rhodacaridae				×	✓		predator	Pugh & King (1988)
Prostigmata								
Eupodidae	*Eupodes minutus* (Strandtman)					×	algae	Gressitt & Shoup (1967)
Halacaridae	*Halacarellus* sp.	×	×				predator	Pugh & King (1985b)
	Isobactrus magnus (Lohmann)	✓	✓	✓	×		algae	
Stigmaeidae	*Eryngiopus* sp.				✓	✓	lichens	
Tydeidae		×				✓	fungi & lichens	Strong (1967), Gressitt & Shoup (1967)
Coleoptera								
Curculionidae	*Bothrometopus parvulus* (Waterhouse)				✓	✓	lichens & detritus	Crafford *et al.* (1986)
	B. randi (Jeannel)			×	×	✓	lichens	Crafford *et al.* (1986)
	Palirhoeus eatoni (Waterhouse)				✓	×	algae	Crafford *et al.* (1986)
Diptera								
	Apetaenus litoralis (Eaton)				✓	×	lichen & detritus	Crafford *et al.* (1986)
Chironomidae	*Telmatogeton amphibius* (Eaton)	✓	✓	×			algae	Strong (1967), Crafford *et al.* (1986)
Hymenoptera								
Eucoilidae	*Kleidotoma icarus* (Quinlan)				✓		parasitoid	Crafford *et al.* (1986)

TABLE 3.2 Variance ratios (VR) of species associations and abundance covariations, n = number of samples, W = test statistic of variance ratio with a chi-square distribution (Schluter 1984).

Species associations

	All species			Algae			Fungi/lichen			Predators			
Zones	**VR**	**W**	**p <**	**VR**	**W**	**p <**	**VR**	**W**	**p <**	**VR**	**W**	**p <**	**n**
Red	1.144	68.64	ns	1.043	62.58	ns	0.977	58.62	ns	1.000	60.00	ns	60
Porphyra	1.243	74.58	ns	1.203	72.18	ns	0.953	57.18	ns	1.000	60.00	ns	60
Verrucaria	1.247	74.82	ns	1.498	89.88	0.05	0.966	57.96	ns	1.000	60.00	ns	60
Mastodia	2.485	149.10	0.01	1.251	75.06	ns	1.769	106.14	0.01	1.236	74.16	ns	60
Caloplaca	1.819	109.14	0.01	0.734	44.04	ns	1.600	96.00	0.01	0.989	59.34	ns	60

Abundance covariation

	All species			Algae			Fungi/ lichen			Predators			
Zones	**VR**	**W**	**p <**	**VR**	**W**	**p <**	**VR**	**W**	**p <**	**VR**	**W**	**p <**	**n**
Red	1.282	76.92	ns	1.282	76.92	ns	0.977	58.62	ns	1.000	60.00	ns	60
Porphyra	0.983	58.98	ns	0.980	58.80	ns	0.977	58.62	ns	1.000	60.00	ns	60
Verrucaria	1.577	94.62	0.01	1.578	94.68	0.01	0.992	59.52	ns	1.000	60.00	ns	60
Mastodia	1.967	118.02	0.01	1.008	60.48	ns	1.093	65.58	ns	1.116	66.96	ns	60
Caloplaca	1.712	102.72	0.01	0.996	59.76	ns	1.231	73.86	ns	1.000	60.00	ns	60

TABLE 3.3 Intraspecific aggregation values of arthropod species in the five habitats on Macaroni Bay. $J_x\%$ = Ives (1991) measure of intraspecific aggregation with the probability of J_x being different from zero based on chi-squared dispersion and the sequential Bonferoni technique (Rice 1989), n = 60 for all tests.

Species	J_x %	Chi-squared	p <
Red zone			
Hyadesia kerguelensis	186.60	14672.57	0.0001
Isobactrus magnus	253.09	3337.51	0.0001
Halozetes marinus devilliersi	166.67	85.00	ns
Halozetes marionensis	322.15	684.97	0.0001
Telmatogeton amphibius	297.83	3982.36	0.0001
***Porphyra* zone**			
Hyadesia kerguelensis	74.45	7299.03	0.0001
Isobactrus magnus	402.74	4014.86	0.0001
Halozetes marionensis	209.12	279.57	0.0001
Telmatogeton amphibius	132.92	363.05	0.0001
***Verrucaria* zone**			
Hyadesia kerguelensis	86.75	5634.77	0.0001
Isobactrus magnus	348.53	6263.78	0.0001
Halozetes marionensis	122.00	676.11	0.0001
***Mastodia* zone**			
Hyadesia halophila	132.51	74427.04	0.0001
Algophagus sp.	699.05	465.45	0.0001
Eryngiopus sp.	355.08	390.23	0.0001
Halozetes marionensis	613.06	6300.94	0.0001
Halozetes belgicae	223.62	77343.55	0.0001
Podacarus auberti	470.93	15972.80	0.0001
Alaskozetes antarcticus	643.52	6984.30	0.0001
Dendrolaelaps sp.	610.06	139.31	0.0001
Rhodacaridae	162.81	239.09	0.0001
Palirhoeus eatoni	305.84	222.09	0.0001
Bothrometopus parvulus	237.28	121.69	0.0001
Apetaenus litoralis	281.00	703.49	0.0001
Kleidotoma icarus	308.16	124.71	0.0001
***Caloplaca* zone**			
Hyadesia halophila	1237.60	2844.60	0.0001
Neocalvolia sp.	838.73	907.12	0.0001
Eryngiopus sp.	157.98	331.72	0.0001
Tydeidae	147.78	138.32	0.0001
Halozetes belgicae	1040.60	1485.63	0.0001
Porokalumma rotunda	874.38	1231.67	0.0001
Dendrolaelaps sp.	6.67	61.00	ns
Bothrometopus randi	837.50	127.00	0.0001
Bothrometopus parvulus	45.50	77.00	ns

TABLE 3.4 Interspecific aggregation values of species in the five habitats identified on Macaroni Bay. $C_{x,-x}$% = Ives (1991) adjusted measure of interspecific aggregation (McGeoch & Chown 1997), and the probability of $C_{x,-x}$ being different from zero based on Spearman rank correlation coefficients (r_s), n = 60 for all tests.

Species	$C_{x,-x}$ %	r_s	p <
Red zone			
Hyadesia kerguelensis	66.32	0.5297	0.0001
Isobactrus magnus	83.13	0.7577	0.0001
Halozetes marinus	25.97	-0.1024	ns
Halozetes marionensis	129.98	0.6164	0.0001
Telmatogeton amphibius	62.38	0.2479	ns
***Porphyra* zone**			
Hyadesia kerguelensis	-6.66	0.0973	ns
Isobactrus magnus	-5.51	0.2068	ns
Halozetes marionensis	30.95	0.3738	0.05
Telmatogeton amphibius	-14.41	-0.1155	ns
***Verrucaria* zone**			
Hyadesia kerguelensis	89.43	0.5736	0.0001
Isobactrus magnus	112.05	0.7963	0.0001
Halozetes marionensis	7.73	0.1333	ns
***Mastodia* zone**			
Hyadesia halophila	137.47	0.4961	0.001
Algophagus sp.	-11.31	0.1267	ns
Eryngiopus sp.	92.80	0.3293	ns
Halozetes marionensis	33.97	0.4939	0.001
Halozetes belgicae	139.14	0.4419	0.01
Podacarus auberti	134.84	0.7002	0.0001
Alaskozetes antarcticus	62.11	0.5881	0.0001
Dendrolaelaps sp.	86.26	0.0811	ns
Rhodacaridae	32.22	0.1522	ns
Palirhoeus eatoni	-47.06	-0.0166	ns
Bothrometopus parvulus	109.07	0.2929	ns
Apetaenus litoralis	83.85	0.2255	ns
Kleidotoma icarus	132.64	0.4080	0.05
***Caloplaca* zone**			
Hyadesia halophila	234.31	0.3972	0.05
Neocalvolia sp.	-34.47	0.0289	ns
Eryngiopus sp.	98.99	0.2760	ns
Tydeidae	-38.23	0.0426	ns
Halozetes belgicae	346.96	0.5033	0.001
Porokalumma rotunda	37.15	0.2923	ns
Dendrolaelaps sp.	0.34	0.0867	ns
Bothrometopus randi	-32.43	0.0214	ns
Bothrometopus parvulus	7.42	0.1887	ns

TABLE 3.5 Interspecific aggregation values of arthropod species in the five zones on Macaroni Bay. C_{xy}% = Ives' (1991) measure of interspecific aggregation with the probability of C_{xy} being different from zero based on Spearman rank correlations and the sequential Bonferoni technique (Rice 1989), n = 60 for all tests.

Species	C_{xy} %	r_s	p <
Red zone			
Hyadesia kerguelensis &			
Isobactrus magnus	76.32	0.7697	0.0001
Halozetes marionensis	107.00	0.5584	0.001
Isobactrus magnus &			
Halozetes marionensis	214.01	0.6639	0.0001
***Verucarria* zone**			
Hyadesia kerguelensis &			
Isobactrus magnus	117.60	0.7737	0.0001
***Mastodia* zone**			
Hyadesia halophila &			
Halozetes marionensis	28.92	0.4652	0.05
Podacarus auberti	132.47	0.6924	0.0001
Alaskozetes antarcticus	56.90	0.5100	0.01
Algophagus sp. &			
Apetaenus litoralis	141.68	0.5042	0.01
Halozetes marionensis &			
Podacarus auberti	233.03	0.6806	0.0001
Alaskozetes antarcticus	302.86	0.7657	0.0001
Halozetes belgicae &			
Podacarus auberti	130.62	0.4670	0.05
Alaskozetes antarcticus	34.31	0.5496	0.001
Podacarus auberti &			
Alaskozetes antarcticus	379.41	0.7715	0.0001
Rhodacaridae &			
Bothrometopus parvulus	162.24	0.5212	0.01
Apetaenus litoralis	81.02	0.5907	0.0001
***Caloplaca* zone**			
Hyadesia halophila &			
Halozetes belgicae	1024.87	0.6401	0.0001

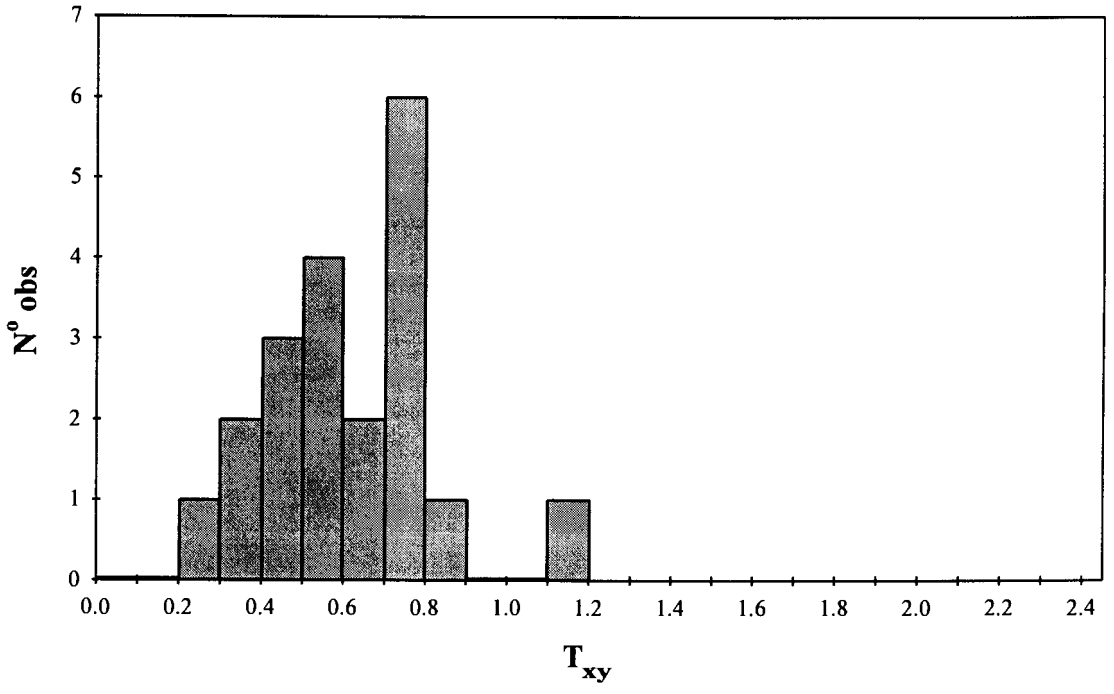

FIG. 3.2 The relative effect of the pairwise aggregation of y on x, T_{xy} for species in the Red zone, median T_{xy} = 0.598; WSR tests p = 0.0001, Z = 3.845, n = 20

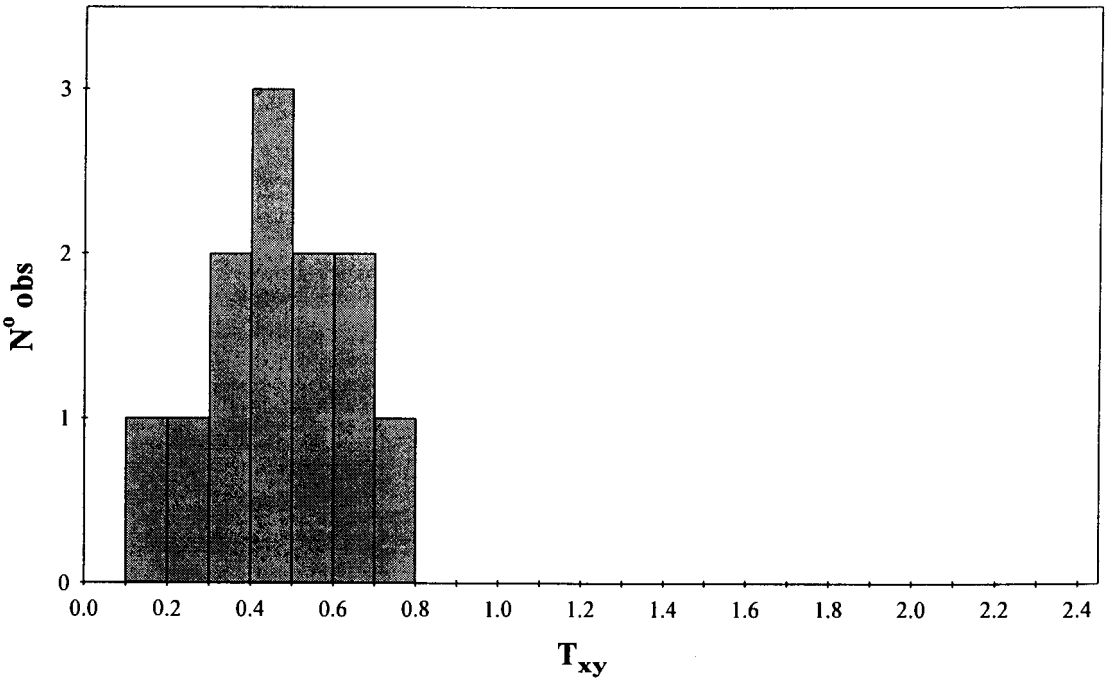

FIG. 3.3 The relative effect of the pairwise aggregation of y on x, T_{xy} for species in the *Porphyra* zone, median T_{xy} = 0.480; WSR tests p = 0.0022, Z = 3.059, n = 12

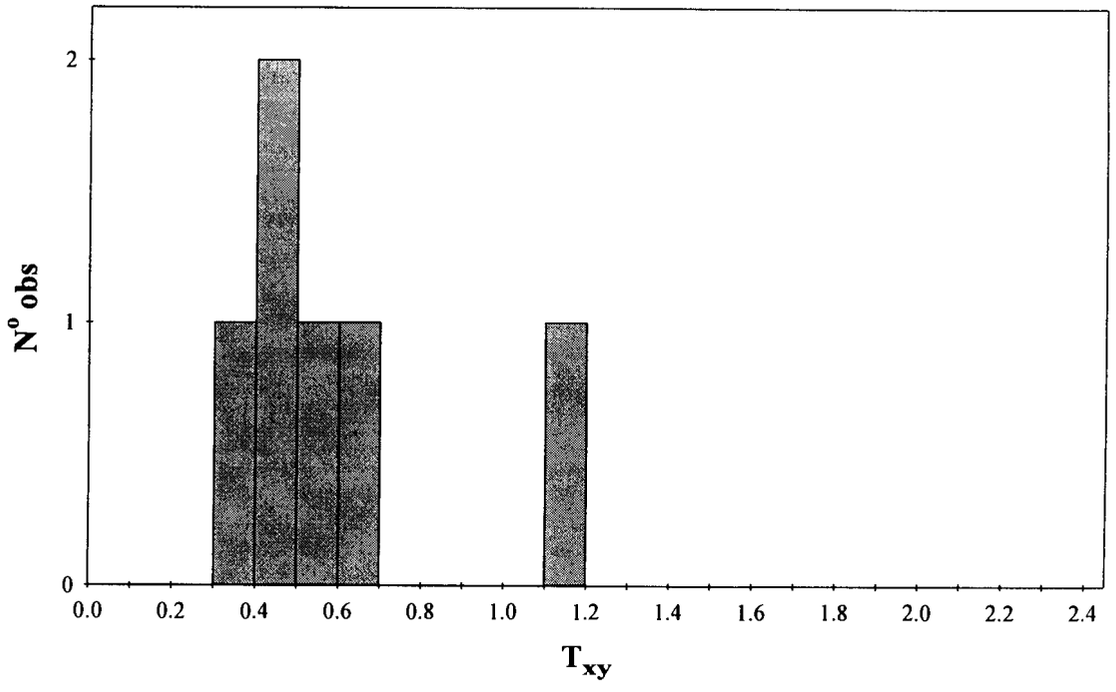

FIG. 3.4 The relative effect of the pairwise aggregation of y on x, T_{xy} for species in the *Verrucaria* zone, median $T_{xy} = 0.501$; WSR tests p = 0.0464, Z = 1.992, n = 6

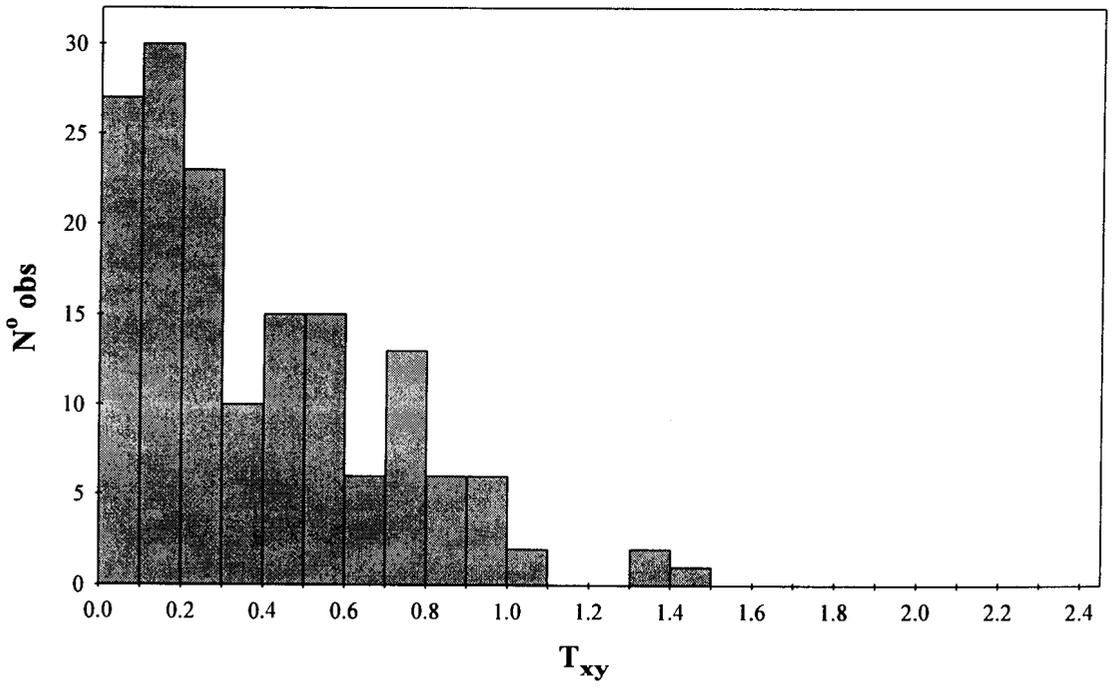

FIG. 3.5 The relative effect of the pairwise aggregation of y on x, T_{xy} for species in the *Mastodia* zone, median $T_{xy} = 0.291$; WSR tests p < 0.0001, Z = 10.620, n = 156

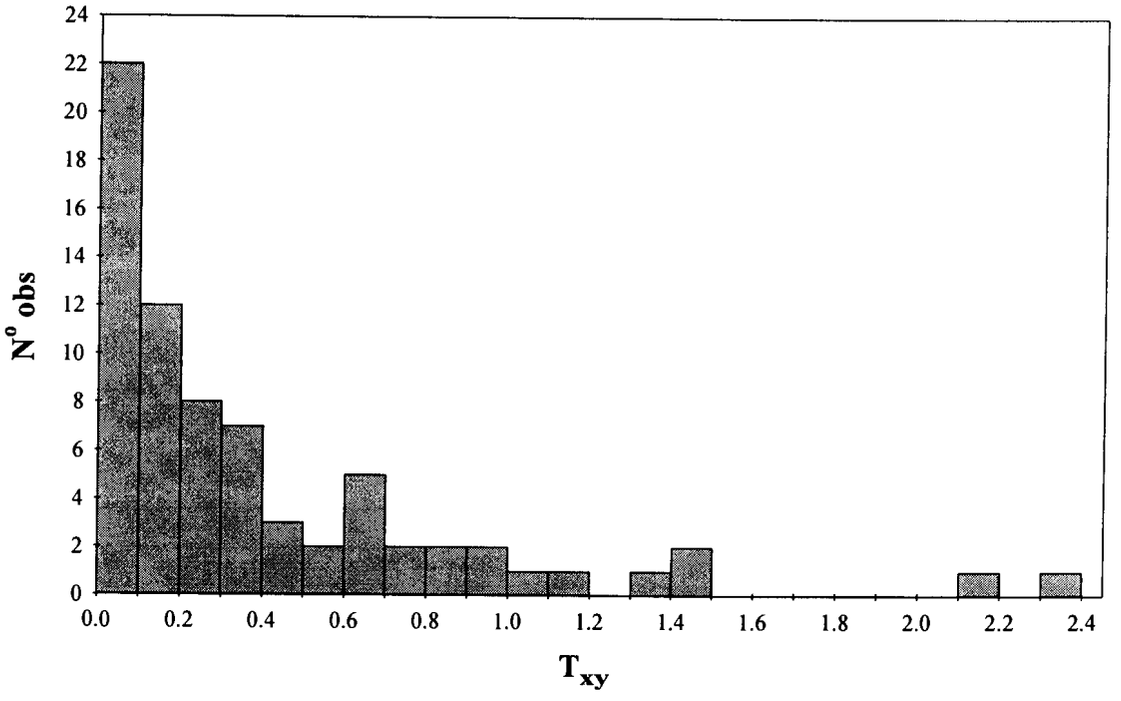

Fig. 3.6 The relative effect of the pairwise aggregation of y on x, T_{xy} for species in the *Caloplaca* zone, median $T_{xy} = 0.237$; WSR tests $p < 0.0001$, $Z = 6.263$, $n = 72$

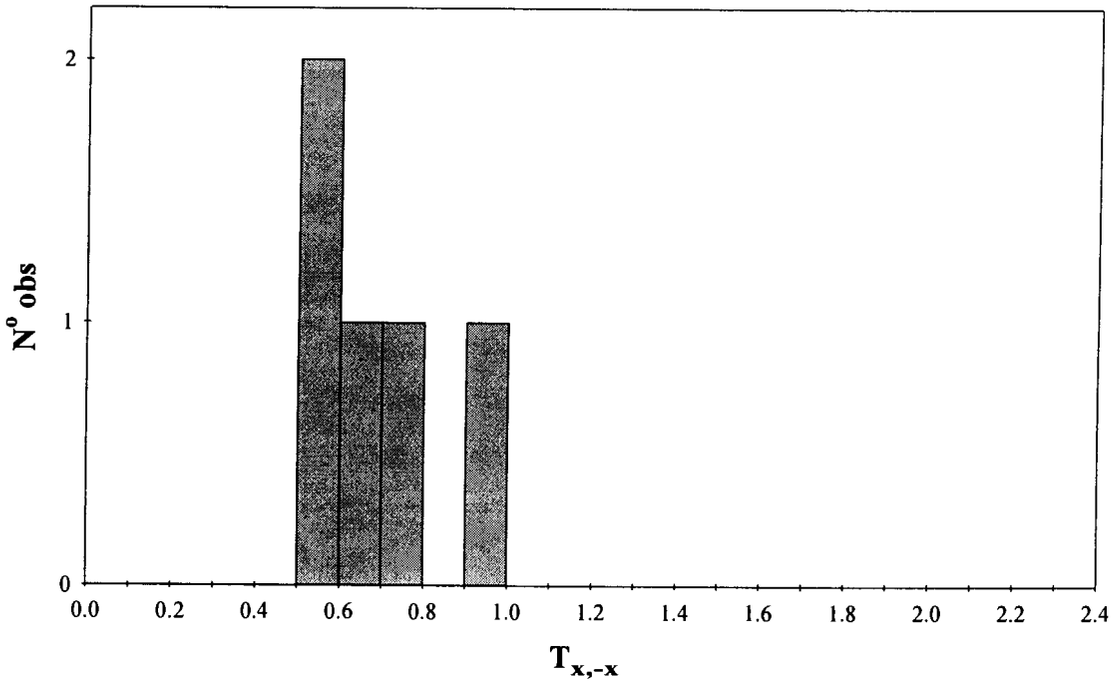

FIG. 3.7 Relative effect of multispecies aggregation on x, $T_{x,-x}$ in Red zone, median $T_{x,-x} = 0.628$; WSR test $p = 0.0431$, $Z = 2.023$, $n = 5$

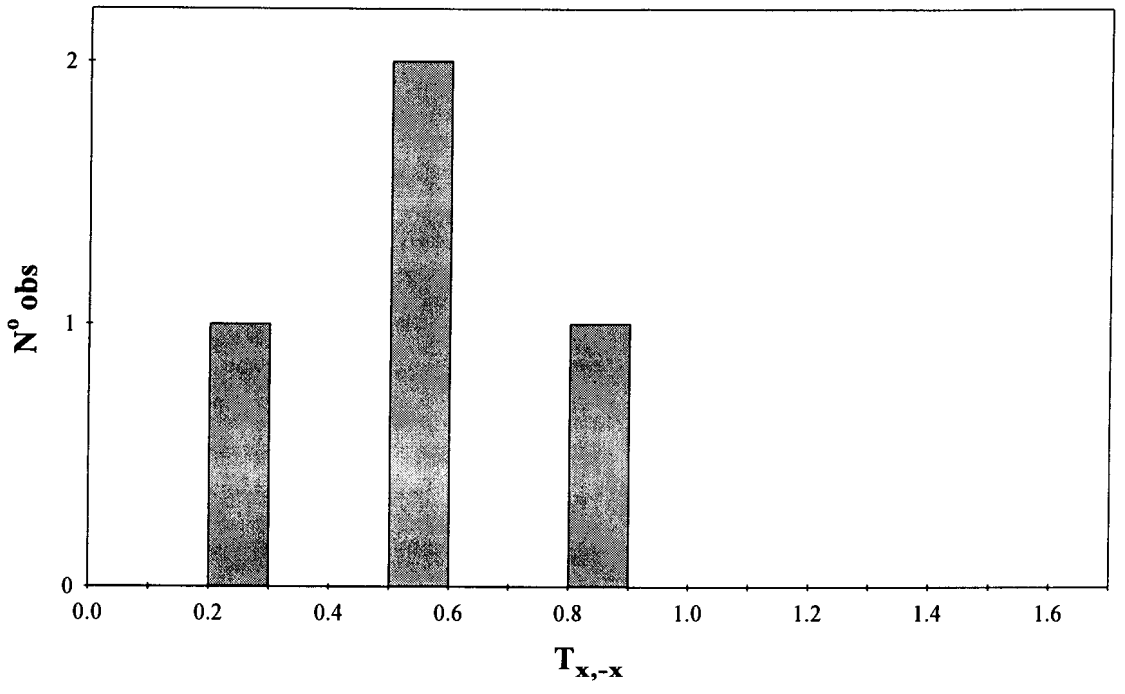

FIG. 3.8 Relative effect of multispecies aggregation on x, $T_{x,-x}$ in the *Porphyra* zone, median $T_{x,-x}$ = 0.542; WSR test p = 0.0679, Z = 1.826, n = 4

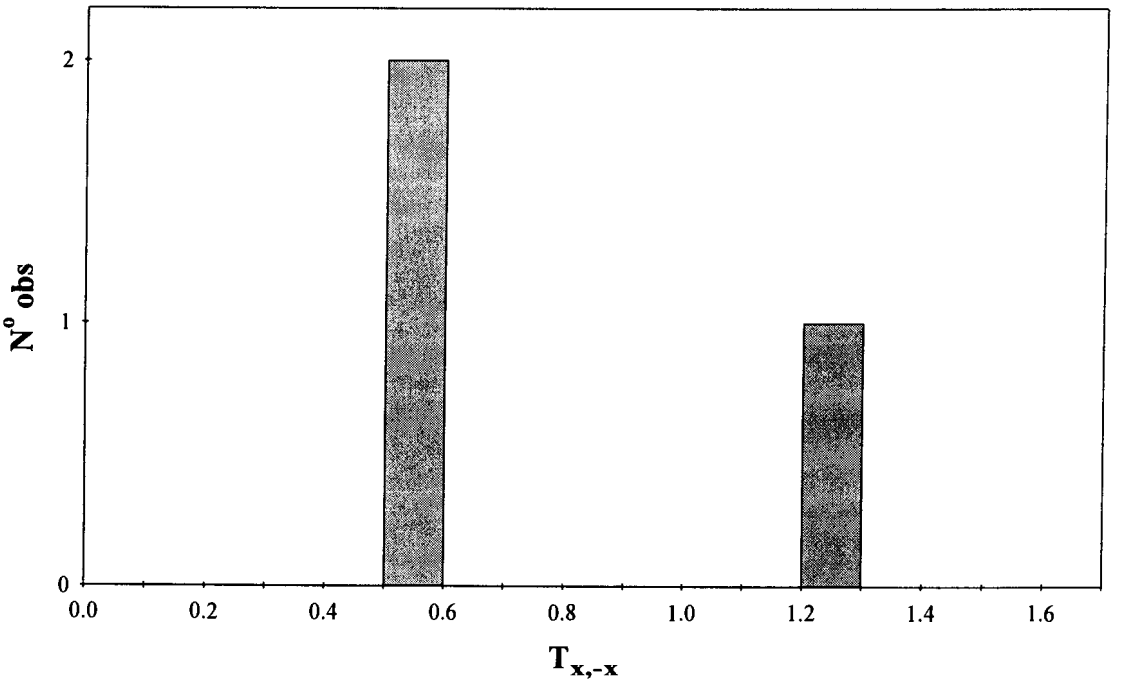

FIG. 3.9 Relative effect of multispecies aggregation on x, $T_{x,-x}$ in the *Verrucaria* zone, median $T_{x,-x}$ = 0.578; WSR test p = 0.2851, Z = 1.069, n = 3

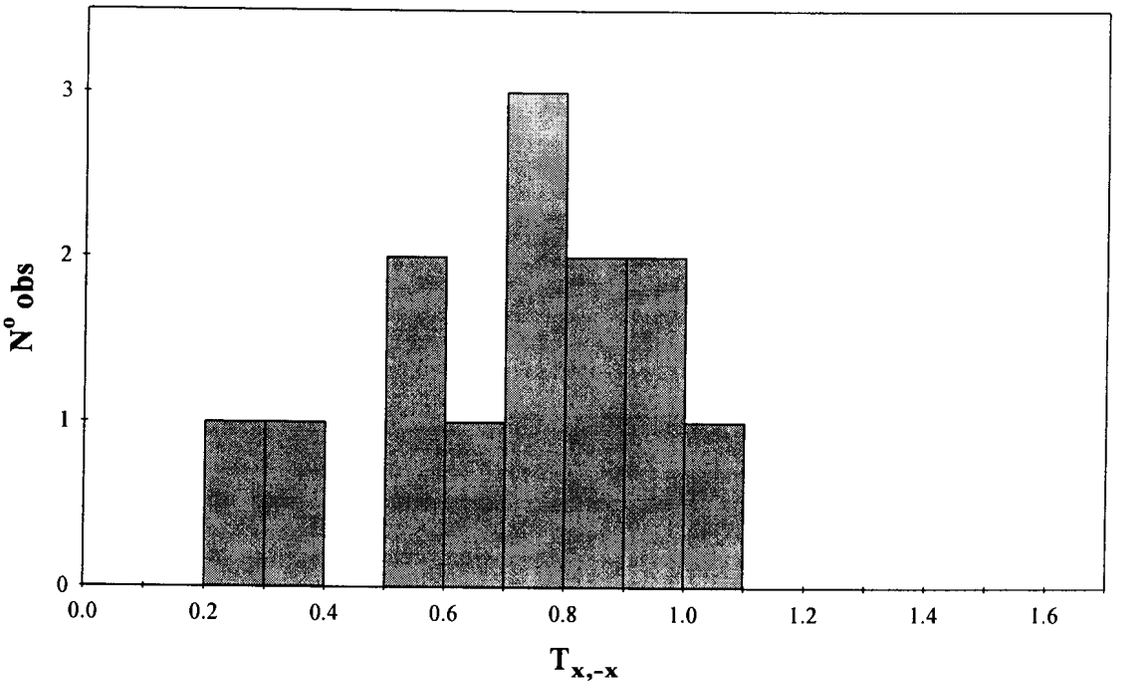

FIG. 3.10 Relative effect of multispecies aggregation on x, $T_{x,-x}$ in the *Mastodia* zone, median $T_{x,-x}$ = 0.760; WSR test p = 0.0024, Z = 3.040, n = 13

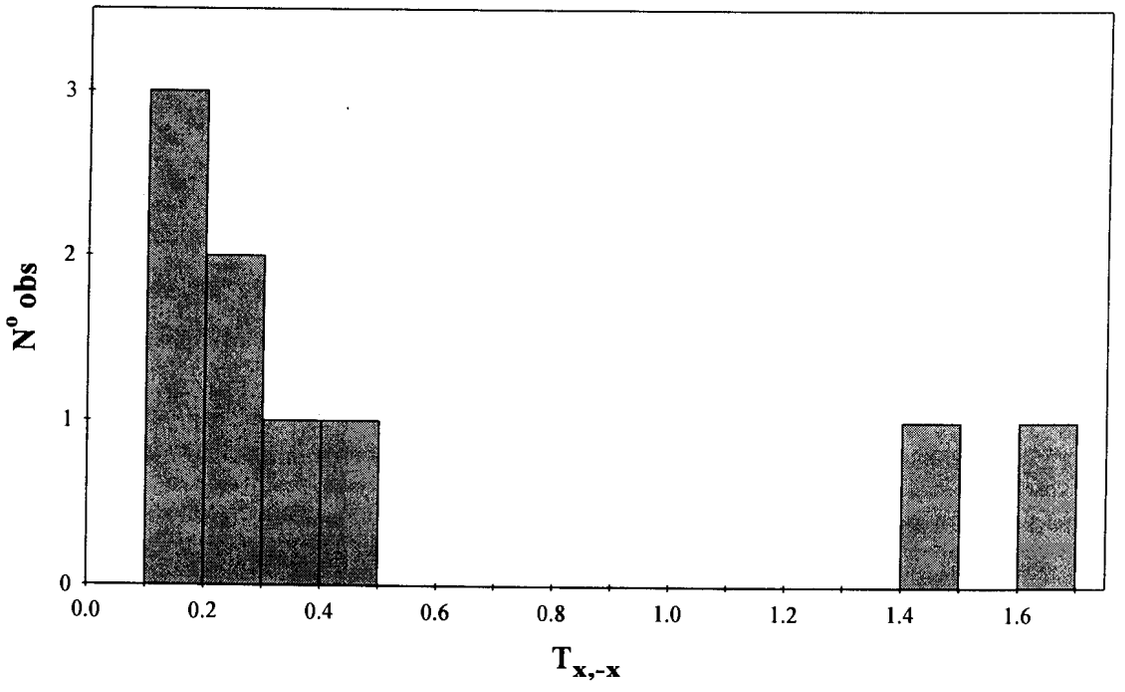

FIG. 3.11 Relative effect of multispecies aggregation on x, $T_{x,-x}$ in the *Caloplaca* zone, median $T_{x,-x}$ = 0.294; WSR test p = 0.0284, Z = 2.192, n = 9

3.4 Discussion

The sloping rocky shore at Macaroni Bay provides an ideal site to study the different process that structure assemblages along an environmental gradient. Mercer *et al.* (in preparation) have previously shown that there is an increase in both diversity and abundance of mites and insects from the littoral to supralittoral habitats on this shore (Fig. 3.1). Species associations and abundance covariation follow the same pattern, with increased interactions in the supralittoral. Greater species diversity in the supralittoral represents more than just higher species richness, with assemblages containing a greater diversity of feeding guilds and trophic levels. Littoral zone assemblages consist mostly of algivore species while in the supralittoral, assemblages contain species feeding on fungi and lichen, a few algivores, predators and a parasitoid component. Increases in diversity should result in more biotic interactions that could lead to the positive relationships seen in these habitats.

Positive variance ratio results indicate that species are associated with each other and that their abundances fluctuate in unison. Schluter (1984) discusses potential interactions that could result in positive outcomes from the variance ratio tests. First, species may enhance the survival of heterospecifics through habitat amelioration (for examples see Bertness & Hacker 1994 for marsh vegetation; Bertness & Callaway 1994 for marine biota). Although this can't be completely disregarded as a possibility, it is unlikely with the current arthropod taxa. Second, predator abundances may fluctuate in positive response to variation in prey abundance. Rhodacaridae were observed to prey on juvenile *Hyadesia halophila* in the *Mastodia* zone, and *Kleidotoma icarus* was noted as parasitising *Apetaenus litoralis* pupae (personal observation). However, no interspecific aggregations were found between predators and known prey species (see Table 3.4 and 3.5). The third possibility is that heterospecifics could be responding in unison to fluctuations of a mutual limiting resource, where an increase in its availability may result in population increases of all species regardless of whether competition is occurring. In harsh environments competitive interactions are hypothesised to be weaker and abiotic factors believed to be more important in structuring communities (Greenslade 1983). This is the most likely cause of the positive results and more support for this idea is provided below.

The *Verrucaria* zone serves as a useful example illustrating the likelihood of resource limitation as the underlying cause of positive abundance covariation and species associations. The positive associations and abundance covariation in the *Verrucaria* are best explained by interactions in the algae feeding guild. This is probably because the species occurring in this zone are predominantly algivorous with few individuals from other guilds (Table 1, see Mercer *et al.* in preparation for densities). The *Verrucaria* zone represents the upper littoral and splash zone on the shore and is predominantly covered by the encrusting growth forms of *Verrucaria* with very little cover available for arthropods (Mercer *et al.* in

preparation). *Hyadesia kerguelensis* and *Isobactrus magnus*, two of the dominant species within the zone, were found to positively aggregated while the distribution of the third species, *Halozetes marionensis*, appeared to be unrelated to either of them. This can be explained by the clumping of *H. halophila* and *I. magnus* around the small lichen thalli within the zone, while *H. marionensis* aggregates into small holes and cracks occurring in the rock. Thus the patterns in mite abundance reflects the patchily distributed cover which the thalli provided.

These explanations may hold equally well for other guilds further up the shore. The positive species associations exhibited by the fungi/lichen guild in the *Mastodia* and *Caloplaca* zones are also likely to be a consequence of species responding to common resources or set of environmental conditions (Schluter 1984). This idea is supported by the Ameronothridae which are all positively aggregated (see Table 3.5), indicating that they are responding to shared resources or favourable abiotic conditions. It may well be that feeding biologies are too coarse and that finer scales need to be employed to pick up on species that could be competing. For example fungivores may be partitioned into species feeding on hyphae and others feeding on spores (D.J. Marshall personal communication).

Patterns of aggregation differed between zones. *T* values were generally lower in the supralittoral when compared to the littoral, indicating higher levels of intraspecific aggregation relative to interspecific aggregation in the *Mastodia* and *Caloplaca* zones. This suggests that the intensity of conspecific aggregation in the supralittoral is higher than in the zones lower down on the shore. Increased intraspecific aggregation should theoretically allow for the coexistence of more competitors in a given habitat (Sevenster & van Alphen 1996). This could also be related to increases in species richness within habitats with high levels of mean crowding. Regardless of whether species are competing for the mutual resources, they do require a certain amount of physical space in which to live. If mean densities reach a saturation level, which may be the case with the high densities in the *Mastodia* zone, then space would become a limiting resource within the habitat. Although the densities of arthropods in the *Caloplaca* zone are lower than the other habitats (see Fig. 3.1), the physical structure of the lichen reduces the amount of available space that can be occupied. The lichen is extremely compact with very little space between thalli. Species are therefore restricted to small patches where the lichen is either less compact or has lifted from the substratum. Therefore, densities are probably higher in the habitable patches than those indicated by Fig. 3.1. Higher levels of intraspecific aggregation, relative to interspecific aggregation, would thus allow species to coexist and explain the high diversity in habitats with high abundances. Conversely, higher intraspecific aggregation could possibility indicate increased levels of competitive interactions.

The positive abundance covariation and species associations indicate that species on the shore respond to resources in similar ways. The increase in both frequency and intensity of these measures from the littoral to the supralittoral zones may be explained by the availability of limiting resources and

increases in the diversity and abundance of arthropods. Based on these indices I have been unable to demonstrate patterns in community structure that could be the result of competitive interactions. However, competitive interactions could still be structuring community patterns, but without careful field experiments there is no evidence to support or refute the idea. Nonetheless, if aggregation does facilitate coexistence, changes up the shore may indicate the operation of this process. Intraspecific was stronger than interspecific aggregation in all five of the zones, fulfilling one of the main requirements for the aggregation model. Biotic interactions were stronger in the supralittoral than littoral habitats suggesting that interactions, possibly competition for space, may be important in structuring the community. Therefore there is some limited evidence in support of Pugh's (1995) idea that the upper limits of a species distribution are influenced partially by biotic interactions. However, this result may simply be a consequence of increased diversity and more field studies are required to verify the importance of biotic interactions in determining species distributions.

3.5 REFERENCES

Atkinson, W.D. & Shorrocks, B. (1984) Aggregation of larval diptera over discrete and ephemeral breeding sites: the implications for coexistence. *American Naturalist* 124:336-351

Begon, M., Harper, J.L. & Townsend, C.R. (1990) *Ecology*. Blackwell Scientific Publications

Bertness, M.D. (1991) Interspecific interactions among high marsh perennials in a New England salt marsh. *Ecology* 72:125-137

Bertness, M.D. & Callaway, R. (1994) Positive interactions in communities. *Trends in Ecology and Evolution* 9:191-193

Bertness, M.D. & Hacker, S.D. (1994) Physical stress and positive associations among marsh plants. *American Naturalist* 144:363-372

Bertness, M.D. & Leonard, G.H. (1997) The role of positive interactions in communities: lessons from intertidal habitats. *Ecology* 78:1976-1989

Chown, S.L. & Steenkamp, H.E. (1996) Body size and abundance in a dung beetle assemblage: optimal mass and the role of transients. *African Entomology* 4:203-212

Crafford, J.E., Scholtz, C.H. & Chown, S.L. (1986) The insects of sub-Antarctic Marion and Prince Edward Islands; with a bibliography of entomology of the Kerguelen Biogeographical Province. *South African Journal of Antarctic Research* 16:41-84

Davenport, J. & MacAlister, H. (1996) Environmental conditions and physiological tolerance of intertidal fauna in relation to shore zonation at Husvik, South Georgia. *Journal of the Marine Biological Association of the United Kingdom* 76:985-1002

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

Dudgeon, S.R., Steneck, R.S., Davison, I.R. & Vadas, R.L. (1999) Coexistence of similar species in a space-limited intertidal zone. *Ecological Monographs* 69:331-352

Gaston, K.J., Blackburn, T.M., Hammond, P.M. & Stork, N.E. (1993) Relationships between abundance and body size: where do tourists fit? *Ecological Entomology* 18:310-314

Giller, P.S. & Doube, B.M. (1994) Spatial and temporal co-occurrence of competitors in Southern African dung beetle communities. *Journal of Animal Ecology* 63:629-643

Greenslade, P.J.M. (1983) Adversity selection and the habitat template. *American Naturalist* 122:352-365

Gressitt, J.L. & Shoup, J. (1967) Ecological notes on free-living mites in North Victoria Land. In: Gressitt, J.L. (ed) *Entomology of Antarctica Vol. 10.* Antarctic Research Series, American Geophysical Union, pp. 307-323

Hanski, I. (1987) Carrion fly community dynamics: patchiness, seasonality and coexistence. *Ecological Entomology* 12:257-266

Hawkins, S.J. & Hartnoll, R.G. (1985) Factors determining the upper limits of intertidal canopy-forming algae. *Marine Ecology Progress Series* 20:265-271

Hay, M. (1981) The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. *Ecology* 78:1990-2003

Heath, D. (1995) *An introduction to experimental design and statistics for biology*. University College London, London

Inouye, B.D. (1999) Integrating nested spatial scales: implications for the coexistence of competitors on a patchy resource. *Journal of Applied Ecology* 68:150-162

Ives, A.R. (1988) Aggregation and the coexistence of competitors. *Annales Zoologici Fennici* 25:75-88

Ives, A.R. (1991) Aggregation and coexistence in a carrion fly community. *Ecological Monographs* 61:75-94

Knox, G.A. (1994) *The biology of the Southern Ocean*. Cambridge University Press, Cambridge

Kouki, J. & Hanski, I. (1995) Population aggregation facilitates coexistence of many competing carrion fly species. *Oikos* 72:223-227

Krantz, G.W. (1978) *A manual of acarology (2nd Edition)*. Corvallis, Oregon State University Book Stores

Lewis, J.R. (1964) *The ecology of rocky shores*. The English University Press, London

Luxton, M. (1990) The marine littoral mites of the New Zealand region. *Journal of the Royal Society of New Zealand* 20:367-418

Marshall, D.J., Gremmen, N.J.M., Coetzee, L., O'Connor, B.M., Pugh, P.J.A., Theron, P.D. & Ueckermann, E.A. (1999) New records of Acari from the sub-Antarctic Prince Edward Islands. *Polar Biology* 21:84-89

Mathieson, A.C. & Nienhuis, P.H. (1990) *Ecosystems of the world 24 - Intertidal and littoral ecosystems*. Elsevier, Amsterdam

McGeoch, M.A. & Chown, S.L. (1997) Evidence of competition in a herbivorous, gall-inhabiting moth (Lepidoptera) community. *Oikos* 78:107-115

Menge, B.A. (1995) Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs* 65:21-74

Mercer, R.D., Chown, S.L. & Marshall, D.J. (in preparation) Mite and insect zonation on a Marion Island rocky shore: a quantitative approach. Submitted to *Polar Biology*

Pugh, P.J.A. (1995) Air breathing littoral mites of sub-Antarctic South Georgia. *Journal of Zoology, London* 236:649-666

Pugh, P.G.A. & King, P.E. (1985a) The vertical distribution of the British intertidal Acari – the non-halacarid fauna (Arachnida: Acari). *Journal of Zoology, London* 207:21-33

Pugh, P.G.A. & King, P.E. (1985b) Feeding in intertidal acari. *Journal of Experimental Marine Biology and Ecology* 94:269-280

Pugh, P.J.A. & King, P.E. (1988) Acari of the British supralittoral. *Journal of Natural History* 22:107-122

Rice, W.R. (1989) Analyzing tables of statistical tests. *Evolution* 43:223-225

Rosewell, J., Shorrocks, B. & Edwards, K. (1990) Competition on a divided and ephemeral resource: testing the assumptions. I. Aggregation. *Journal of Animal Ecology* 59:977-1001

Russel, G. (1990) Vertical distribution. In: Mathieson, A.C., Nienhuis, P.H. (eds) *Ecosystems of the world 24 - Intertidal and littoral ecosystems*. Elsevier, Amsterdam, pp 43-65

Schluter, D. (1984) A variance test for detecting species associations, with some example implications. *Ecology* 65:998-1005

Sevenster, J.G. (1996) Aggregation and coexistence. I. Theory and analysis. *Journal of Animal Ecology* 65:297-307

Sevenster, J.G. & van Alphen, J.J.M. (1996) Aggregation and coexistence. II. A neotropical *Drosophila* community. *Journal of Animal Ecology* 65:308-324

Shorrocks, B., Rosewell, J. & Edwards, K. (1990) Competition on a divided and ephemeral resource: testing the assumptions. II. Association. *Journal of Animal Ecology* 59:1003-1017

Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*. Third Edition. W.M. Freeman, New York

Stephenson, T.A. & Stephenson, A. (1972) *Life between tidemarks on rocky shores*. W.H. Freeman and Company, San Francisco

Strauss, S.Y. (1991) Indirect effects in community ecology: their definition, study and importance. *Trends in Ecology and Evolution* 6:206-209

Strong, J. (1967) Ecology of terrestrial arthropods at Palmer Station, Antarctic Peninsula. In: Gressitt, J.L. (ed) *Entomology of Antarctica Vol. 10*. Antarctic Research Series, American Geophysical Union, pp. 357-371

Toda, M.J., Kimura, M.T. & Tuno, N. (1999) Coexistence mechanisms of mycophagous drosophilids on mutlispecies fungal hosts: aggregation and resource partitioning. *Journal of Animal Ecology* 68:794-803

Wootton, J.T. (1993) Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. *American Naturalist* 141:71-89

APPENDIX

- Ives' (1991) measures of intraspecific aggregation:

$$J_x = \left\{ \left[\sum_{i=1}^{L} n_i (n_i - 1)/(NL) \right] - N \right\} / N$$

and interspecific aggregation:

$$C_{xy} = \left\{ \left[\sum_{i=1}^{L} n_i m_i /(NL) \right] - M \right\} / M$$

where n_i and m_i are the numbers of individuals of species x and y in habitat unit i. N and M denote the mean number of individuals of species x and y across L number of samples (Ives 1991).

- Relative effect of aggregation is defined by the inequality (Sevenster 1996):

$$T_{xy} = \frac{(1 + C_{xy})}{(1 + J_y)} < 1$$

where T_{xy} is defined as the 'relative effect of aggregation of y on x. The order of x and y in the subscript of T_{xy} is important because T_{xy} is interpreted as the effect of y on x, therefore T_{xy} is different to T_{yx}.

- Variance ratio tests after Schluter (1984)

$$VR = S_T{}^2 / \sum \sigma_i{}^2$$

$$S_T{}^2 = (1/N) \sum_{j}^{N} (T_j - t)^2$$

Presence/absence data (species associations):

$$\sigma_i{}^2 = p_i (1 - p_i)$$

where $p_i = n_i/N$, n_i is the total number of samples in which a species i is found, T_j is the total number of species in sample j, t is the observed mean number of species per sample. N is the total number of samples respectively.

Population density data (abundance covariation):

$$\sigma_i^2 = (1/N) \sum_{j}^{N} (X_{ij} - t_i)^2$$

where X_{ij} is the density of species i in sample j, and t_i is the observed mean density of species i.

CHAPTER 4 INVERTEBRATE BODY-SIZES FROM MARION ISLAND – LOCAL AND REGIONAL IMPLICATIONS

4.1 INTRODUCTION

Body size is an important animal characteristic which is correlated with most physiological and life history variables (Peters 1983), it may be used as a convenient surrogate for these traits. Thus body sizes provide useful preliminary indications of the likely characteristics of a given set of species or assemblage (Gaston & Blackburn in press). Consequently, body size has been the subject of numerous ecological and physiological studies (e.g. Peters 1983; Schmidt-Nielsen 1984; Brown *et al.* 1993; Atkinson & Sibly 1997; Kosłowski & Weiner 1997), and is recognised as an important macroecological variable (Blackburn *et al.* 1990; Blackburn & Gaston 1999).

Despite a substantial literature on the systematics, ecology and physiology of invertebrates from the sub-Antarctic and Antarctic (see e.g. Block 1984; Frenot *et al.* 1989; Greenslade 1990; Pugh 1993; Chown 1994; Convey 1997; Starý & Block 1998; Vernon *et al.* 1998; Bergstrom & Chown 1999; Davies & Melbourne 1999; Hänel & Chown 1999), information on this important biological variable is not readily available, at least not in a compiled format. Given that ecologists and physiologists apparently record body sizes as frequently as journalists report people's ages (Nee & Lawton 1996), that the value of compendia of body sizes is being increasingly recognised (Blackburn & Gaston 1994), and the such compendia being made available (Silva & Downing 1995) this constitutes an important lacuna in current knowledge regarding invertebrates.

The general absence of compiled data on invertebrate body sizes is not just a phenomenon of Antarctic research, but extends to faunas elsewhere. In the past, only a few studies have sought to compile insect body sizes, and these generally had the goals either of calculating one measure of body mass from another (e.g. Rogers *et al.* 1976), or of understanding habitat-associated variation in body sizes (e.g. Schoener & Janzen 1968). More recently, and with the rise of macroecology (Brown 1995; Gaston & Blackburn in press), numerous studies have given attention to invertebrate body size patterns (e.g. Morse *et al.* 1988; Currie & Fritz 1993; Hawkins 1995; Hawkins & Lawton 1995; Chown & Gaston 1999; Siemann *et al.* 1999; Walter & Behan-Pelletier 1999). With a few exceptions, and usually because of the species richness of invertebrate assemblages and journal space constraints, these works rarely consider the entire local fauna or report the original body size data.

Nonetheless, the former goal has long been of interest to ecologists (see e.g. May 1978; Loder *et al.* 1997), while the latter is clearly required for reaching it. Because Antarctic and sub-Antarctic invertebrate

faunas tend to be relatively species poor (e.g. Block 1984; Greenslade 1990; Pugh 1993), they lend themselves to entire documentation, thus making this goal possible. Providing a compilation of body sizes for the invertebrates of the region, or at least assemblages within it, may be considered a research priority both for this reason and because it is likely to provide some indication of the characteristics of assemblages from remote Antarctic/sub-Antarctic sites that are currently known mainly or exclusively from collections (see e.g. Vernon & Voisin 1990; Davies *et al.* 1997; Convey & Lewis Smith 1997).

Here I make a start at addressing these issues by providing a compilation of body sizes of the most common invertebrate species from Marion Island. This compilation not only includes body size measures for virtually all the insect, spider, springtail, and molluscan species known from the island, but also includes information on the most common mite species, and regression equations which may assist future workers in estimating body mass of these and related species from linear dimensions.

4.2 Methods

Body size measures were obtained in two ways. First, data on insects and spiders were collated from studies undertaken on Marion Island (46°54'S, 37°45'E) between 1986 and 1998. Rather than using published data from these works, the raw data were retrieved and re-analysed for consistency. In most of these studies, fresh body mass had been measured using a Mettler AE163 electronic microbalance (precision of 0.1 mg) or Mettler UMT2 electronic ultrabalance (precision of 0.1 μg), and dry mass obtained after invertebrates had been dried to constant mass. Linear dimensions were also generally obtained from measurements using an ocular micrometer mounted on a Wild M3B dissecting microscope.

Second, a variety of invertebrate species (especially mites, springtails, spiders and molluscans) were weighed and measured specifically for this study. For mites, springtails and smaller insects fresh mass was measured using a Mettler UMT2 electronic ultrabalance (precision of 0.1 μg), while a Mettler AE163 electronic microbalance (precision of 0.1 mg) was used for the larger taxa (e.g. earthworms and insects). Linear dimensions were measured using an ocular micrometer mounted on a Wild M3B dissecting microscope, and all measurements (except for the larger invertebrates) were made at 40x magnification.

Acari were individually weighed on the Mettler ultrabalance, except for *Erynetes* sp., where five individuals were weighed together (3.3 μg), and *Nanorchestes* sp., where 10 individuals were weighed together (4.6 μg, 4.2 μg and 4.7 μg, n = 3 groups). These weights were divided by the number of individuals to obtain a mean body mass per mite. Body size was measured as the total body length from the gnathosoma to the posterior margin of the notogaster.

Collembola, with the exception of *Megalothorax* sp., were weighed individually and measured (length from the anterior head to posterior abdomen). For *Megalothorax* sp. five individuals were

weighed simultaneously and the resultant weight divided by five to obtain a mean mass per individual. The mass/length regression for the collembola was calculated using mean body mass and length for each species, while the fresh/dry mass regression used data from individual specimens.

For all other taxa mass was calculated on an individual basis (with the exception of the Enchytraeidae, where several individuals were weighed together and the mass then divided by n). On the whole, body size was measured as the length from the anterior margin of the eye to final abdominal segment except for some taxa and life stages where other measures were employed. In the case of insect larvae, head capsules were measured at their widest point and used as an indication of size. In the case of the spiders, measurements were taken from the anterior to posterior margins of the cephalothorax. The shells of *Notodiscus hookeri* were measured across the widest diagonal from the lip of the shell aperture. All body sizes were expressed in millimetres (mm).

Dry masses were calculated from specimens dried to constant mass for four days at 60°C. These results although not given as means ± SE, were used to calculate the fresh/dry mass relationships for selected taxa. Least squares linear regressions were performed on log transformed data to examine the relationships between fresh body mass (g) and body length (mm), and between fresh and dry body mass (g).

4.3 Results & Discussion

Body sizes were measured for 59 of the approximately 120 known invertebrate species found on Marion Island (see Crafford *et al.* 1986; Chown *et al.* 1998; Marshall *et al.* 1999; Gabriel 1999). Although the 19 mite taxa that were measured represent less than one third of the acarine diversity, they do represent 17 of the 28 families (see Marshall *et al.* 1999). The remaining 40 species that were measured represented more than 80% of the non-acarine taxa. Species not measured during the course of the study were either rare, unconfirmed records or undescribed species (especially in the case of the mites - see Marshall *et al.* 1999). Therefore, the species in this study are regarded as being representative of the entire invertebrate fauna found on Marion Island, and certainly sufficient for obtaining relationships that can be used to estimate body sizes of taxa known from only a few specimens (e.g. Bartsch 1999).

Mean fresh body masses and body lengths (including headcapsule widths, cephalothorax lengths and shell diameters) are provided for the Acari, Collembola, insects and other invertebrates in Tables 4.1 - 4.3. Within each of the three major taxonomic groups, body mass spanned three orders of magnitude (Acari from 0.0005 to 0.5206 mg; adult insects from 0.03 to 26.17 mg; and Collembola from 0.0008 to 0.5088 mg) with five orders of magnitude covered across all taxonomic groups. Body length ranges are more difficult to compare because different parameters were measured for species (see Methods) and only

selected taxa were measured. However, the range does span two orders of magnitude, from 0.1 mm (*Nanorchestes* sp. - Table 4.1) to over 10 mm for *Paractora dreuxi mirabilis* (Crafford *et al.* 1986).

Although altitudinal variation in body size has been documented for some insect species on Marion Island (e.g. Chown 1992), this variation did not form a topic of investigation here, largely because data from different altitudes were not consistently available. However, one such case is reported, that of *Myro paucispinosus* (Araneae) because differences between individuals collected at high (> 800 m) and mid to low altitudes (< 500 m) were considerable (Table 4.3). Indeed, there is a large range of body sizes in this spider species, with the heaviest high altitude specimen (185 mg) weighing almost an order of magnitude more than the second largest one (54 mg). This stresses the need for further examinations of both altitudinal and gender-related variation in body size of invertebrates on Marion Island, and the underlying causes of this variation (see Chown & Scholtz 1989; Chown 1992; Chown & Smith 1993; van der Merwe *et al.* 1997; for data on and discussions of this kind of variation in ectemnorhine weevils).

For those taxa with sufficient data, mass-length regressions and fresh-dry mass regressions were calculated (Table 4.4 - 4.6). All regression equations are expressed in grams (g) and millimeters (mm) with the only exception being the mites, where, for convenience, the mass units are micrograms ($\mu g = 10^{-6}$ g). Both interspecific and intraspecific (insects only) regressions were positive and significant, and there were no outliers that warranted removal. Slopes of the intraspecific body length-body mass regressions for the different insect species were significantly different (ANCOVA $p < 0.001$), suggesting that for prediction of body mass it may be useful to use regressions from within the lowest taxonomic rank possible. However, it is clearly not necessary to do so for the species in this study! Thus, to broaden the applicability of these results, the regressions were extended to the family, order and class levels (Table 4.5). Due to differences in slope of the relationships at the different levels (between families ANCOVA $p < 0.001$; between orders ANCOVA $p = 0.0117$), I recommend that the regressions for the lowest possible rank in the taxonomic hierarchy still be used.

In the case of the mites, however, slopes of the interspecific body length/body mass regressions for each of the four mite orders (Mesostigmata, Cryptostigmata, Prostigmata and Astigmata) were not significantly different (ANCOVA, $p = 0.7306$), and therefore the combined regression can be used with confidence for estimating body mass of mites from body length. At the interspecific level, and perhaps unsurprisingly, body length/body mass regressions for the collembola, mites and insects also had significantly different slopes (ANCOVA $p < 0.001$).

Rogers *et al.* (1976) found that for insects the relationship between dry weight (W in mg) and length (L in mm) could be described by the equation $W = 0.0305 \log L^{2.62}$. The slope of this relationship is significantly less than the one found here (3.15 ± 0.026, $t = 20.38$, $p < 0.001$, see Sokal & Rohlf 1995 for details of the test). This is undoubtedly due to the broader range of taxa measured by Rogers *et al.* (1976).

The latter authors examined species from 59 families and nine orders (weight range 0.02 - 800 mg, length range 0.5 - 36 mm), whereas I examined 11 species from seven families and five orders (weight range 0.03 - 18 mg, length range 0.98 - 7.26 mm) (see Table 4.3). This difference in mass/length equations raises the question of how broadly applicable our results (or those of Rogers *et al.* 1976) are to insects in the Antarctic region as the whole. Because the families I used in this study are representative of the insect fauna for Marion and other sub-Antarctic and Antarctic islands, and because Antarctic insect faunas are generally disharmonic (i.e. major taxa common to continents are missing, see Chown *et al.* 1998), in my view the present regression equations for insects should be used in preference to the one presented by Rogers *et al.* (1976). However, because most of the major springtail and mite taxa are represented in the Antarctic/sub-Antarctic, the regressions presented for these species should be considered more broadly applicable, at least until further data can be brought to bear on the problem.

In conclusion, in this study I have presented a broad compilation of information on body sizes of a sub-Antarctic invertebrate assemblage that should prove useful for estimating body sizes for other, similar taxa in the Antarctic, especially from sites where the invertebrates are known from collections only. In addition, I hope that this data compilation will stimulate further such studies from other Antarctic/sub-Antarctic areas. The provision of such information from other areas should enable macroecological work on invertebrate taxa (and especially the Acari and Collembola), something that is comparatively rare (see Chown & Gaston 1999; Gaston & Chown 1999; Gaston & Blackburn in press). In addition, it will provide baseline information on an important trait that seems to be changing, in many species, in step with rapid local and global environmental changes (see Chown & Smith 1993; Block & Harrisson 1995; Ernsting *et al.* 1995; see also Smith *et al.* 1998).

TABLE 4.1 Mean fresh body mass (mg) and body length (mm) for Acari on Marion Island. Bracketed *n* denote the number of individuals weighed together to get a single mass. A - adults, N - nymphs, Lv - larvae

Order / Family	Species	Stage	Fresh mass (mg)			Body length (mm)			n
			mean ± SE	min	max	mean ± SE	min	max	
Mesostigmata									
Rhodacaridae	-----	A/N	0.1011 ± 0.0111	0.0123	0.2254	0.90 ± 0.0371	0.38	1.26	29
Cillibidae	-----	A/N	0.0215 ± 0.0010	0.0132	0.0280	0.56 ± 0.0090	0.45	0.61	19
Cryptostigmata									
Peloppiidae	*Macquarioppia striata*	A	0.0416 ± 0.0060	0.0314	0.0550	0.62 ± 0.0217	0.57	0.67	4
Oppiidae	*Austroppia crozetensis*	A	0.0055 ± 0.0002	0.0048	0.0067	0.28 ± 0.0047	0.26	0.31	10
Oribatulidae	*Dometorina marionensis*	A	0.0109 ± 0.0009	0.0058	0.0171	0.42 ± 0.0072	0.38	0.45	15
Ameronothridae	*Alaskozetes antarcticus*	A	0.1601 ± 0.0080	0.1329	0.2113	0.98 ± 0.0206	0.90	1.10	10
		N	0.0679 ± 0.0114	0.0081	0.1338	0.69 ± 0.0497	0.36	0.90	15
		Lv	0.0063 ± 0.0007	0.0047	0.0083	0.34 ± 0.0161	0.29	0.38	5
	Halozetes belgicae	A	0.0325 ± 0.0013	0.0218	0.0456	0.61 ± 0.0073	0.55	0.67	20
		N	0.0069 ± 0.0005	0.0045	0.0090	0.33 ± 0.0105	0.29	0.38	9
		Lv	0.0027 ± 0.0004	0.0023	0.0030	0.24 ± 0.0060	0.24	0.25	2
	H. fulvus	A	0.0314 ± 0.0009	0.0251	0.0409	0.62 ± 0.0044	0.58	0.67	22
	H. marinus	A	0.0948 ± 0.0017	0.0574	0.1302	---	---	---	58
	H. marionensis	A	0.0666 ± 0.0021	0.0502	0.0774	0.74 ± 0.0086	0.67	0.79	20
		N	0.0269 ± 0.0054	0.0074	0.0572	0.55 ± 0.0357	0.38	0.71	9
	Podacarus auberti	A	0.1950 ± 0.0059	0.1690	0.2325	1.16 ± 0.0103	1.11	1.19	11
		N	0.1388 ± 0.0240	0.0371	0.2394	0.92 ± 0.0682	0.60	1.17	11
		Lv	0.0107	---	---	0.43	---	---	1

TABLE 4.1 continued

Order / Family	Species	Stage	Fresh mass (mg)			Body length (mm)			n
			mean ± SE	min	max	mean ± SE	min	max	
Prostigmata									
Nanorchestidae	*Nanorchestes* spp.	A/N	0.0005	---	---	0.14	0.14	0.14	3 (10)
Rhagidiidae	*Rhagidia* sp.	A/N	0.0180 ± 0.0005	0.0175	0.0185	0.61 ± 0.5952	0.62	0.01	2
Halacaridae	*Isobactrus magnus*	A/N	0.0168 ± 0.0017	0.0044	0.0270	0.43 ± 0.0199	0.29	0.52	18
Ereynetidae	*Ereynetes* sp.	A/N	0.0007	---	---	0.17	---	---	1 (5)
Bdellidae	*Bdellodes* sp.	A/N	0.0522 ± 0.0170	0.0090	0.1552	0.66 ± 0.0886	0.33	1.12	8
Stigmaeidae	*Eryngiopus* sp.	A/N	0.0102 ± 0.0015	0.0018	0.0180	0.42 ± 0.0228	0.31	0.50	10
Erythreidae	*Balaustium* sp.	A	0.5206	---	---	1.643	---	---	1
Astigmata									
Hyadesiidae	*Hyadesia halophila*	A/N	0.0131 ± 0.0010	0.0039	0.0265	0.39 ± 0.0111	0.26	0.50	26

TABLE 4.2 Mean fresh body mass (mg) and body length (mm) for the Collembola on Marion Island. Bracketed *n* denote the number of individuals weighed together to get a single mass.

Family	Species	Fresh mass (mg)				Body length (mm)			
		mean ± SE	min	max	n	mean ± SE	min	max	n
Hypogastruridae	*Ceratophysella denticulata*	0.0201 ± 0.0025	0.0070	0.0520	20	1.08 ± 0.0463	0.74	1.39	20
Onychiuridae	*Tullbergia bisetosa*	0.0882 ± 0.0094	0.0200	0.1540	20	1.31 ± 0.0571	0.93	1.85	20
Isotomidae	*Cryptopygus antarcticus travei*	0.0441 ± 0.0054	0.0240	0.1140	20	2.15 ± 0.0879	1.60	2.87	20
	C. dubius	0.0058 ± 0.0006	0.0030	0.0140	20	0.68 ± 0.0257	0.46	0.83	20
	Isotoma marionensis	0.0128 ± 0.0007	0.0060	0.0200	20	1.54 ± 0.0290	1.39	1.85	20
	I. notabilis	0.0097 ± 0.0004	0.0070	0.0160	20	0.83 ± 0.0289	0.58	1.16	20
	I. palustris	0.0792 ± 0.0196	0.0100	0.4230	20	2.59 ± 0.0852	1.88	3.33	20
Tomoceridae	*Pogonognathellus flavescens*	0.5088 ± 0.0824	0.1810	1.5330	20	2.96 ± 0.1376	2.03	4.06	20
Neelidae	*Megalothorax* sp.	0.0008 ± 0.0001	0.0004	0.0014	20 (5)	0.28 ± 0.0129	0.12	0.35	20
Sminthuridae	*Katianna* sp.	0.0256 ± 0.0028	0.0090	0.0620	20	0.56 ± 0.0394	0.37	1.01	20
	Sminthurinus granulosus	0.0518 ± 0.0062	0.0270	0.1210	20	1.39 ± 0.0696	0.93	1.90	20
	S. tuberculatus	0.0076 ± 0.0004	0.0040	0.0110	20	0.37 ± 0.0292	0.18	0.65	20

TABLE 4.3 Mean fresh body mass and mean body length for the insects and other invertebrates on Marion Island. # - species used to calculate the insect mass/length regression, A - adults, P - pupae, Lv - larvae, Imm - immatures, * - headcapsule width (mm), § - cephalothorax length (mm), ‡ - maximum shell diagonal (mm), ¥ - mean weights from variable number of individuals (1-40) weighed to get a single mass.

Order / Family	Species	Stage	Fresh mass (mg)				Body length (mm)			
			mean ± SE	min	max	n	mean ± SE	min	max	n
Hemiptera										
Aphidoidea	*Rhapalosiphum padi* #	A?	0.2759 ± 0.0200	0.0340	0.7000	64	0.98 ± 0.2433	0.74	1.47	3
Thysanoptera										
Thripidae	*Apterothrips apteris* #	A	0.0393 ± 0.0017	0.0058	0.0640	40	1.11 ± 0.0410	0.90	1.55	19
Coleoptera										
Hydraenidae	*Meropathus chuni* #	A	0.5577 ± 0.0264	0.4572	0.6916	10	2.24 ± 0.0453	2.07	2.45	10
		Lv	0.1353 ± 0.0224	0.0913	0.1642	3	1.63 ± 0.1675	1.29	1.82	3
Staphylinidae	*Halmaeusa atriceps* #	A	0.8002 ± 0.0331	0.0610	1.4000	49	3.00	3.00	3.00	1
		P	0.4215	---	---	1	---	---	---	---
		Lv	0.4059 ± 0.0234	0.0590	0.9000	59	3.48 ± 0.1665	3.24	3.80	3
Curculionidae	*Bothrometopus parvulus* #	A	4.5441 ± 0.1211	2.0400	8.7800	119	4.05 ± 0.0689	3.53	4.59	22
	B. randi #	A	18.0877 ± 0.7477	9.0100	36.1400	90	7.26 ± 0.1553	5.66	8.36	22
	B. elongatus #	A	1.7149 ± 0.0756	0.9700	12.4000	155	2.89 ± 0.0337	2.47	3.29	45
		Lv	1.6629 ± 0.4658	0.5360	5.1000	9	0.48 ± 0.0269 *	0.38 *	0.60 *	9
	Ectemnorhinus spp. #	A	16.8326 ± 0.5588	1.9000	42.0500	235	6.18 ± 0.0706	3.06	8.36	235
		P	24.8263 ± 9.2165	6.6790	36.7000	3	7.75 ± 0.0500	7.70	7.80	2
		Lv	5.7173 ± 0.4883	0.1100	39.1000	209	0.64 ± 0.0169 *	0.24 *	1.20 *	209
	Ectemnorhinus marioni	A	12.3286 ± 0.5996	5.5100	24.5000	80	---	---	---	---
		Lv	7.7079 ± 1.1813	0.1680	48.5000	62	0.60 ± 0.0213 *	0.26 *	1.10 *	102
	Ectemnorhinus similis	A	23.4954 ± 0.8407	8.5000	41.1600	76	---	---	---	---
		Lv	7.3968 ± 1.3860	0.0140	24.1000	28	0.66 ± 0.0276 *	0.29 *	1.06 *	61
	Palirhoeus eatoni #	A	7.3126 ± 0.2105	4.2200	12.6800	90	4.54 ± 0.0828	3.93	5.57	29

TABLE 4.3 continued

Order / Family	Species	Stage	Fresh mass (mg) mean ± SE	min	max	n	Body length (mm) mean ± SE	min	max	n
Diptera										
Physchodidae	*Pyschoda parthenogenetica*	A	0.2450 ± 0.0981	0.0282	0.9000	8	---	---	---	---
		P	0.7000	---	---	1	---	---	---	---
		Lv	0.3790 ± 0.1229	0.0554	0.9000	6	---	---	---	---
Chironomidae	*Telmatogeton amphibius* #	A	1.0843 ± 0.1156	0.4370	2.6120	23	2.38 ± 0.1457	1.65	4.63	23
		Lv	0.9864 ± 0.1609	0.0100	5.0460	51	0.36 ± 0.0220 *	0.12 *	0.62 *	51
	Limnophyes minimus	A	0.1298 ± 0.0155	0.0207	0.2286	18	---	---	---	---
		P	0.2468 ± 0.0283	0.0431	0.5222	15	---	---	---	---
		Lv	0.2286 ± 0.0166	0.0710	0.4077	34	0.17 ± 0.0033 *	0.17 *	0.18 *	3
Helcomyzidae	*Paractora dreuxi mirabilis*	A	12.2375 ± 0.8395	4.2000	25.4000	40	---	---	---	---
		Lv	41.8186 ± 0.7383	14.1000	94.2000	339	---	---	---	---
Drosophilidae	*Scaptomyza* sp.	A	2.1333 ± 0.2536	0.6000	3.3000	12	---	---	---	---
		P	0.9000	---	---	1	---	---	---	---
Tethinidae	*Apetaenus litoralis*	A	1.9022 ± 0.0866	0.1710	3.7000	66	2.75 ± 0.3725	1.76	3.82	6
		Lv	3.5855 ± 0.1635	1.4000	9.0000	69	---	---	---	---
Calliphoridae	*Calliphora vicina*	A	55.9160 ± 4.1340	21.1000	101.2000	19	---	---	---	---
		Lv	81.5330 ± 4.1800	67.1000	106.9000	9	---	---	---	---

TABLE 4.3 continued

Order / Family	Species	Stage	Fresh mass (mg)				Body length (mm)			
			mean ± SE	min	max	n	mean ± SE	min	max	n
Lepidoptera										
Tineidae	*Pringleophaga marioni*	A	26.1739 ± 2.2546	11.0000	47.0000	18	---	---	---	---
		P	72.1667 ± 9.5694	0.6000	146.7000	15	1.50 ± 0.5271	0.49	2.26	3
		Lv	23.8443 ± 2.7929	0.2510	178.9000	141	1.32 ± 0.1164	0.29	3.30	42
Yponomeutidae	*Embryonopsis halticella*	A	3.8290 ± 0.3550	2.1000	6.1000	14	---	---	---	---
		Lv	1.6520 ± 0.2330	0.0740	14.7700	122	---	---	---	---
	Plutella xylostella	A	9.7080 ± 5.8920	1.9000	74.4000	12	---	---	---	---
		Lv	7.1540 ± 0.6820	2.7000	11.9000	13	---	---	---	---
Hymenoptera										
Eucoilidae	*Kleidotoma icarus* #	A	0.3184 ± 0.0236	0.1760	0.4900	13	1.98 ± 0.0454	1.68	2.26	13
Arachnida										
	Myro paucispinosus (high)	A	36.2069 ± 8.0757	11.459	185.000	21	2.84 ± 0.1337 §	2.03 §	4.00 §	20
	Myro paucispinosus (low)	A	10.1752 ± 2.1501	0.0444	57.200	32	---	---	---	---
	Myro kerguelensis	A	1.3422 ± 0.0950	0.532	2.593	20	0.56 ± 0.0280 §	0.289 §	0.863 §	20
	Erigone spp.	A?	0.639 ± 0.0598	0.0223	3.4000	113	---	---	---	---
Gastropoda										
Stylommatophor	*Notodiscus hookeri*	A	35.0143 ± 2.7907	16.153	54.121	20	5.02 ± 0.1654 ‡	3.62 ‡	6.08 ‡	20
	Deroceras caruanae	A	137.216 ± 5.5869	103.973	185.118	20	---	---	---	---
Haplotaxida										
Lumbricidae	*Microscolex kerguelensis*	A?	218.9 ± 11.2	139.1	316.6	6	---	---	---	---
		Imm?	24.300 ± 1.700	1.0	76.3	14	---	---	---	---
Enchytraeidae		A?	0.8423 ± 0.0367	0.0785	2.68	20 (¥)	---	---	---	---

TABLE 4.4 Intraspecific relationships between fresh mass and body size (or head capsule width) for the Acari, collembola and selected insect species from Marion Island, with regression results. A - adults, N - nymphs, Lv - larvae, Mμg - mass (μg), M - mass (g), L - body length (mm), Hc - head capsule width (mm), Sd - shell diameter (mm), w - known fresh mass (μg), x - known length (mm), y - known head capsule width (mm), z - known fresh mass (g), s - known shell diameter.

Taxa	Stage	Equation	SE of int.	SE of slope	SE of est.	R^2	n	p
Apterothrips apteris	A	log M = -4.441 + 1.205 log x	0.0153	0.2032	0.0561	0.6739	19	0.00002
		log L = 2.498 + 0.559 log z	0.4146	0.0944	0.0382			
Meropathus chuni	A	log M = -4.241 + 3.189 log x	0.3604	1.148	0.3449	0.4909	10	0.0240
		log L = 0.805 + 0.154 log z	0.1838	0.0554	0.0758			
Telmatogeton amphibius	A	log M = -3.500 + 1.343 log x	0.1108	0.2932	0.1492	0.4997	23	0.00016
		log L = 1.484 + 0.372 log z	0.2454	0.0813	0.0785			
Telmatogeton amphibius	Lv	log M = -1.913 + 2.984 log y	0.0853	0.1537	0.2327	0.8998	44	< 0.0001
		log Hc = 0.526 + 0.302 log z	0.0543	0.0155	0.0739			
Pringleophaga marioni	Lv	log M = -2.189 + 3.052 log y	0.0364	0.1442	0.1954	0.9412	30	< 0.0001
		log Hc = 0.678 + 0.308 log z	0.0317	0.1456	0.0621			
Kleidotoma icarus	A	log M = -4.479 + 3.398 log x	0.1497	0.4566	0.0674	0.8343	13	< 0.0001
		log L = 1.154 + 0.246 log z	0.1139	0.0329	0.0181			
Bothrometopus elongatus	A	log M = -3.551 + 1.555 log x	0.1025	0.2222	0.0502	0.5324	45	< 0.0001
		log L = 1.431 + 0.342 log z	0.1388	0.0489	0.0235			
B. elongatus	Lv	log M = -1.701 + 3.636 log y	0.2349	0.7088	0.1459	0.7899	9	0.00135
		log Hc = 0.302 + 0.217 log z	0.1226	0.0424	0.0357			
B. parvulus	A	log M = -3.944 + 2.640 log x	0.3265	0.5371	0.0846	0.5597	21	< 0.0001
		log L = 1.104 + 0.212 log z	0.1012	0.0431	0.0239			
B.randi	A	log M = -4.057 + 2.864 log x	0.1535	0.1785	0.0368	0.9279	22	< 0.0001
		log L = 1.377 + 0.324 log z	0.0324	0.0202	0.0124			

TABLE 4.4 continued

Taxa	Stage	Equation	SE of int.	SE of slope	SE of est.	R^2	n	p
Ectemnorhinus spp.	A	log M = -4.141 + 2.943 log x	0.0375	0.0475	0.0566	0.9427	235	< 0.0001
		log L = 1.371 + 0.320 log z	0.0096	0.0052	0.0187			
Ectemnorhinus spp.	Lv	log M = -1.803 + 3.481 log y	0.0144	0.0509	0.1254	0.9577	209	< 0.0001
		log Hc = 0.486 + 0.275 log z	0.0107	0.0040	0.0353			
E. marioni	Lv	log M = -1.570 + 3.684 log y	0.0433	0.1392	0.1781	0.9248	59	< 0.0001
		log Hc = 0.374 + 0.251 log z	0.0248	0.0095	0.0465			
E. similis	Lv	log M = -1.662 + 3.413 log y	0.0683	0.2578	0.1955	0.8841	25	< 0.0001
		log Hc = 0.405 + 0.259 log z	0.0482	0.0196	0.0539			
Palirhoeus eatoni	A	log M = -4.074 + 2.967 log x	0.1496	0.2278	0.0503	0.8627	29	< 0.0001
		log L = 1.275 + 0.291 log z	0.0476	0.0223	0.0158			
Notodiscus hookeri	A	log M = -3.202 + 2.467 log s	0.0931	0.1331	0.0380	0.9502	20	< 0.0001
		log Sd = 1.268 + 0.385 log z	0.0310	0.0208	0.0150			

TABLE 4.5 Interspecific relationships between fresh mass and body size for the mites, springtails, insects and spiders from Marion Island, with regression results. A - adults, N - nymphs, Lv - larvae, Mμg - mass (μg), M - mass (g), L - body length (mm), Lthx - cephalothorax length (mm), w - known fresh mass (μg), x - known length (mm), z - known fresh mass (g), v - known cephalothorax length (mm).

Taxa	Stage	Equation	SE of int.	SE of slope	SE of est.	R^2	n	p
Acari (all spp.)	A/N/Lv	log Mμg = 2.117 + 2.711 log x	0.0104	0.0333	0.1053	0.9595	281	< 0.0001
		log L = -0.760 + 0.354 log w	0.0067	0.0044	0.0381			
Astigmata	A/N/Lv	log Mμg = 2.143 + 2.550 log x	0.0719	0.1714	0.0563	0.9022	26	< 0.0001
		log L = -0.799 + 0.354 log w	0.0261	0.0238	0.0210			
Cryptostigmata	A/N/Lv	log Mμg = 2.146 + 2.77 log x	0.0103	0.0357	0.0814	0.9738	164	< 0.0001
		log L = -0.760 + 0.351 log w	0.0072	0.0045	0.0289			
Mesostigmata	A/N/Lv	log Mμg = 2.064 + 2.857 log x	0.0198	0.1067	0.9499	0.9397	48	< 0.0001
		log L = -0.687 + 0.329 log w	0.0212	0.0123	0.0322			
Prostigmata	A/N/Lv	log Mμg = 2.124 + 2.808 log x	0.0467	0.1107	0.1505	0.9401	43	< 0.0001
		log L = -0.733 + 0.335 log w	0.0165	0.0132	0.0519			
Collembola (all spp.)	A	log M = -4.678 + 1.851 log x	0.1146	0.3656	0.3962	0.7161	12	0.0005
		log L = 1.815 + 0.387 log z	0.3615	0.0770	0.1811			
Insects (all spp.)	A	log M = -4.294 + 3.151 log x	0.0179	0.0262	0.1225	0.9719	421	< 0.0001
		log L = 1.343 + 0.309 log z	0.0061	0.0026	0.0383			
Curculionidae	A	log M = -4.1783 + 2.9977 log x	0.0190	0.0258	0.0651	0.9747	352	< 0.0001
		log L = 1.3770 + 0.3252 log z	0.0057	0.0028	0.0214			
Coleoptera	A	log M = -4.1929 + 3.0160 log x	0.0217	0.0298	0.0857	0.9659	363	< 0.0001
		log L = 1.3672 + 0.3203 log z	0.0066	0.0032	0.0279			
Spiders (all spp.)	A	log M = -2.415 +1.838 log v	0.0144	0.0384	0.0884	0.9837	40	< 0.0001
		log Lthx = 1.294 + 0.535 log z	0.0262	0.0112	0.0477			

TABLE 4.6 Relationship between fresh and dry body mass in selected taxa. A - adults, P - pupae, L - larvae, Imm - immatures, M - fresh mass, Dm - dry mass, m - known dry mass (g), z - known fresh mass (g).

Taxa	Stage	Equation	SE of Int.	SE of slope	SE of est.	R^2	n	p
Insects (all spp.)	A/P/L	log M = 0.6111 + 1.0213 log m	0.0197	0.0063	0.1693	0.9612	1075	< 0.0001
		log Dm = -0.6930 + 0.9411 log z	0.0152	0.0058	0.1625			
Collembola (all spp.)	A	log M = 0.0504 + 0.9547 log m	0.1033	0.0209	0.1887	0.8977	240	< 0.0001
		log Dm = -0.5499 + 0.9402 log z	0.0962	0.0206	0.1873			
Myro spp.	A	log M = 0.7575 + 1.0731 log m	0.0529	0.0185	0.0731	0.9889	40	< 0.0001
		log Dm = -0.7219 + 0.9215 log z	0.0372	0.0159	0.0677			
Notodiscus hookeri	A	log M = 0.6918 + 1.1139 log m	0.0863	0.0441	0.0282	0.9726	20	< 0.0001
		log Dm = -0.6576 +0.8731 log z	0.0516	0.0345	0.0249			
Deroceras caruanae	A	log M = -0.2264 + 0.3848 log m	0.1871	0.1116	0.0630	0.3976	20	0.00288
		log Dm = -0.7727 + 1.0333 log z	0.2616	0.2998	0.1033			
Oligochaeta (all spp.)	A / Imm	log M = 0.9282 + 1.0899 log m	0.0857	0.0268	0.1638	0.9775	40	< 0.0001
		log Dm = -0.9010 + 0.8968 log z	0.0578	0.0221	0.1486			

4.4 REFERENCES

Atkinson, D. & Sibly, R.M. (1997) Why are organisms usually larger in colder environments? Making sense of a life history puzzle. *Trends in Ecology and Evolution* 12:235-239

Bartsch, I. (1999) *Peregrinacarus reticulatus gen. nov. spec. nov.*, a freshwater halacarid mite from Marion Island. *Hydrobiologia* 392:225-232

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

Blackburn, T.M. & Gaston, K.J. (1994) The distribution of body sizes of the world's bird species. *Oikos* 70:127-130

Blackburn, T.M. & Gaston, K.J. (1999) The relationship between animal abundance and body size: a review of the mechanisms. *Advances in Ecological Research* 28:181-210

Blackburn, T.M., Harvey, P.H. & Pagel, M.D. (1990) Species number, population density and body size relationships in natural communities. *Journal of Animal Ecology* 59:335-345

Block, W. (1984) Terrestrial microbiology, invertebrates and ecosystems. *Antarctic Ecology* 1:163-236

Block, W. & Harrisson, P.M. (1995) Collembolan water relations and environmental change in the maritime Antarctic. *Global Change Biology* 1:347-359

Brown, J.H. (1995) *Macroecology.* University of Chicago Press, Chicago

Brown, J.H., Marquet, P.A. & Taper, M.L. (1993) Evolution of body size: consequences of an energetic definition of fitness. *American Naturalist* 142:573-584

Chown, S.L. (1992) A preliminary analysis of weevil assemblages in the sub-Antarctic: local and regional patterns. *Journal of Biogeography* 19:87-98

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

Chown, S.L., & Gaston, K.J. (1997) The species-body size distribution: energy, fitness and optimality. *Functional Ecology* 11:365-375

Chown, S.L. & Gaston, K.J. (1999) Exploring links between physiology and ecology at macro-scales: the role of respiratory metabolism in insects. *Biological Review* 74:87-120

Chown, S.L., Gremmen, N.J.M. & Gaston, K.J. (1998) Ecological biogeography of Southern Ocean islands: species-area relationships, human impacts and conservation. *American Naturalist* 152:562-575

Chown, S.L. & Scholtz, C.H. (1989) Biology and ecology of the *Dumoecetes* Jeannel (Col. Curculionidae) species complex on Marion Island. *Oecologia* 80:93-99

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

Convey, P. (1997) How are the life history strategies of Antarctic terrestrial invertebrates influenced by extreme environmental conditions. *Journal of Thermal Biology* 22:429-440

Convey, P. & Lewis Smith, R.I. (1997) The terrestrial arthropod fauna and its habitats in northern Marguerite Bay and Alexander Island, maritime Antarctica. *Antarctic Science* 9:12-26

Crafford, J.E., Scholtz, C.H. & Chown, S.L. (1986) The insects of sub-Antarctic Marion and Prince Edward Islands; with a bibliography of entomology of the Kerguelen Biogeographical Province. *South African Journal of Antarctic Research* 16:41-84

Currie, D.J. & Fritz, J.T. (1993) Global patterns of animal abundance and species energy use. *Oikos* 67:56-68

Davies, K.F., Greenslade, P. & Melbourne, B.A. (1997) The invertebrates of sub-Antarctic Bishop Island. *Polar Biology* 17:455-458

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

Ernsting, G., Block, W., MacAlister, H. & Todd, C. (1995) The invasion of the carnivorous carabid beetle *Trechisibus antarcticus* on South Georgia (sub-Antarctic) and its effect on the endemic herbivorous beetle *Hydromedion sparsutum*. *Oecologia* 103:34-42

Frenot, Y., Vernon, P. & Bellido, A. (1989) A bibliography of terrestrial ecosystems on Iles Crozet, Indian Ocean. *Polar Record* 25:121-130

Gabriel, A.G.A. (1999) *The systematics and ecology of the Collembola of Marion Island, sub-Antarctic*. Unpublished MSc Thesis, University of Durban-Westville, South Africa

Gaston, K.J. & Blackburn, T.M. (in press) *Pattern and Process in Macroecology*. Blackwell Science, Oxford

Gaston, K.J. & Chown, S.L. (1999) Elevation and climatic tolerance: a test using dung beetles. *Oikos* 86:584-590

Greenslade, P. (1990) Notes on the biogeography of the free-living terrestrial invertebrate fauna of Macquarie Island with an annotated checklist. *Proceeding of the Royal Society of Tasmania* 124:35-50

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

Hawkins, B.A. (1995) Latitudinal body-size gradients for the bees of the eastern United States. *Ecological Entomology* 20:195-198

Hawkins, B.A. & Lawton, J.H. (1995) Latitudinal gradients in butterfly body sizes: is there a general pattern? *Oecologia* 102:31-36

Kozłowski, J. & Weiner, J. (1997) Interspecific allometries are by-products of body size optimization. *American Naturalist* 149:352-380

Loder, N.S., Blackburn, T.M. & Gaston, K.J. (1997) The slippery slope: towards an understanding of the body size frequency distribution. *Oikos* 78:195-201

Marshall, D.J., Gremmen, N.J.M., Coetzee, L., O'Connor, B.M., Pugh, P.J.A., Theron, P.D. & Ueckermann, E.A. (1999) New records of Acari from the sub-Antarctic Prince Edward Islands. *Polar Biology* 21:84-89

May, R.M. (1978) The dynamics and diversity of insect faunas. In: Mound, L.A. & Waloff, N. (eds) *Diversity of insect faunas*. Blackwell Scientific, Oxford, pp. 188-204

Morse, D.R., Stork, N.E. & Lawton, J.H. (1988) Species number, species abundance and body length relationships of arboreal beetles in Bornean lowland rain forest trees. *Ecological Entomology* 13:25-37

Nee, S. & Lawton, J.H. (1996) Ecology – body-size and biodiversity. *Nature* 380:672-673

Peters, R.H. (1983) *The ecological implications of body size*. Cambridge University Press

Pugh, P.J.A. (1993) A synonymic catalogue of the Acari from Antarctica, the sub-Antarctic Islands and the Southern Ocean. *Journal of Natural History* 27:323-421

Rogers, L.E., Hinds, W.T. & Buschbom, R.L. (1976) A general weight vs. length relationship for insects. *Annals of the Entomological Society of America* 69:387-389

Schoener, T.W. & Janzen, D.H. (1968) Notes on environmental determinants of tropical versus temperate insect size patterns. *American Naturalist* 102:207-244

Schmidt-Nielson, K. (1984) *Scaling: Why Is Animal Size So Important?* Cambridge University Press

Siemann, E., Tilman, D. & Haarstad, J. (1999) Abundance, diversity and body size: patterns from a grassland arthropod community. *Journal of Animal Ecology* 68:824-835

Silva, M. & Downing, J.A. (1995) The allometric scaling of density and body mass: a non-linear relationship for terrestrial mammals. *American Naturalist* 145:704-727

Smith, F.A., Browning, H. & Shepherd, U.L. (1998) The influence of climate change on the body mass of woodrats Neotoma in an arid region of New Mexico, USA. *Ecography* 21:140-148

Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*. Third Edition. W.M. Freeman, New York.

Starý, J. & Block, W. (1998) Distribution and biogeography of oribatid mites (Acari: Oribatida) in Antarctica, the sub-Antarctic islands and nearby land areas. *Journal of Natural History* 32:861-894

van der Merve, M., Chown, S.L. & Smith, V.R. (1997) Thermal Tolerance Limits in six weevil species (Coleoptera, Curculionidae) from sub-Antarctic Marion Island. *Polar Biology* 18:331-336

Vernon, P., Vannier, G. & Trehen, P. (1998) A comparative approach to the entomological diversity of polar regions. *Acta Oecologia* 19:303-308

Vernon, P. & Voisin, J. (1990) Faune entomologique de la Grande Ile des Apotres (Archipel Crozet, Ocean Indien Austral). *Bulletin Societe entomologique Francaise* 95:263-268

Walter, D.E. & Behan-Pelletier, V. (1999) Mites in forest canopies: filling the size distribution shortfall. *Annual Review of Entomology* 44:1-19

CHAPTER 5 SYNTHESIS

The predominant theme running through this work is that quantitative data are more useful than qualitative data in community studies. Carefully collected quantitative data allow for the accurate assessment of species abundances and distributions, where fine scale variation can be easily quantified. Such fine scale variation may not be detectable when using qualitative data and subtle changes in ecosystem functioning may be overlooked. The invertebrate faunas of the sub-Antarctic islands are relatively species poor (e.g. Block 1984; Greenslade 1990; Pugh 1993) making them ideal systems for examining whole community structure and processes. Current research trends in the Antarctic and sub-Antarctic are focussing on global climatic change, the introduction of alien species and their combined effects on ecosystem functioning (e.g. Lewis Smith 1990; Chown & Smith 1993; Block & Harrisson 1995; Ernsting *et al.* 1995; Simpson *et al.* 1995; Gremmen 1997; Chown *et al.* 1998; Hänel & Chown 1998; Bergstrom & Chown 1999; Davies & Melbourne 1999). These isolated and species poor islands are sensitive to slight perturbations making them ideal models for global systems. However, to accurately determine the impact that perturbations have on these islands high quality baseline data for future monitoring must be acquired (e.g. see Lewis Smith 1990).

Although there is a considerable amount of literature on the taxonomy, distribution and physiology of the invertebrate taxa from the Antarctic and sub-Antarctic (see Frenot *et al.* 1989; Block 1992; Hänel & Chown 1999) the global importance of these fragile ecosystems is only now being realised. This thesis has highlighted, and tried to address, those areas of research that were previously lacking. The most important idea to emerge from this entire thesis is that data should be presented in such a format that it is readily accessible to a wider audience than just the author/s. By generating good quality quantitative data and presenting it in such a manner that comparisons can be made across studies, understanding of how Antarctic and sub-Antarctic ecosystems function, can be readily achieved. Besides these general conclusions a number of specific research possibilities were also identified.

1. Similar quantitative studies on other sub-Antarctic islands will enable more robust hypothesis testing on the nature of species interactions, alien invasions and the effects that climatic conditions, both past and present, have on community structure (e.g. see Smith *et al.* 1998).
2. Although species interactions were believed to be weak in the sub-Antarctic (Block 1984) current research is showing that species interactions do occur (e.g. Ernsting *et al.* 1995). Understanding how species interact with heterospecifics, and even conspecifics, in the community is vital if predictions about community changes are to be made. Quantifying species interactions for the entire island will be possible using the data collected from the other M.I.T.I.E. studies (see Gabriel 1999; Hänel 1999;

Barendse 2000), and the variance ratio tests and species association measures described in Chapter 3. Undertaking such studies will allow previous hypotheses regarding sub-Antarctic ecosystems to be tested in a more rigorous fashion.

3. Carefully collected and archived data is extremely flexible with broad range applicability and can be combined easily with other studies. For the first time body-sizes have been calculated for an entire assemblage, and together with the abundance and distribution data, from this and other M.I.T.I.E. studies, many macroecological theories regarding species body size - abundance - distributions can be tested on an entire ecosystem (see Blackburn *et al.* 1990; Blackburn & Gaston 1999).

5.1 REFERENCES

Barendse, J. (2000) *Patterns in the distribution and abundance of terrestrial arthropods on sub-Antarctic Marion Island*. MSc Thesis, University of Pretoria

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

Blackburn, T.M. & Gaston, K.J. (1999) The relationship between animal abundance and body size: a review of the mechanisms. *Advances in Ecological Research* 28:181-210

Blackburn, T.M., Harvey, P.H. & Pagel, M.D. (1990) Species number, population density and body size relationships in natural communities. *Journal of Animal Ecology* 59:335-345

Block, W. (1984) Terrestrial microbiology, invertebrates and ecosystems. In: Laws R.M. (ed) *Antarctic Ecology, Vol. 1*. Academic Press, London, pp. 163-236

Block, W. (1992) *An annotated bibliography of Antarctic invertebrates (terrestrial and freshwater)*. British Antarctic Survey, Cambridge

Block, W. & Harrisson, P.M. (1995) Collembolan water relations and environmental change in the maritime Antarctic. *Global Change Biology* 1:347-359

Chown, S.L., Gremmen, N.J.M. & Gaston, K.J. (1998) Ecological biogeography of Southern Ocean islands: species-area relationships, human impacts and conservation. *American Naturalist* 152:562-575

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

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

Ernsting, G., Block, W., MacAlister, H. & Todd, C. (1995) The invasion of the carnivorous carabid beetle *Trechisibus antarcticus* on South Georgia (sub-Antarctic) and its effect on the endemic herbivorous beetle *Hydromedion sparsutum*. *Oecologia* 103:34-42

Frenot, Y., Vernon, P. & Bellido, A. (1989) A bibliography of terrestrial ecosystems on Iles Crozet, Indian Ocean. *Polar Record* 25:121-130

Gabriel, A.G.A. (1999) *The systematics and ecology of the Collembola of Marion Island, sub-Antarctic*. MSc Thesis, University of Durban-Westville

Greenslade, P. (1990) Notes on the biogeography of the free-living terrestrial invertebrate fauna of Macquarie Island with an annotated checklist. *Proceeding of the Royal Society of Tasmania* 124:35-50

Gremmen, N.J.M. (1997) Changes in the vegetation of sub-Antarctic Marion Island resulting from introduced vascular plants. In: Battaglia, B., Velencia, J. & Walton, D.W.H. (eds) *Antarctic communities: species, structure and survival*. Cambridge University Press, Cambridge, pp. 417-423

Hänel, C. (1999) *The distribution and abundance of macro-invertebrates in the major vegetation communities on Marion Island and the impact of alien species*. MSc Thesis, University of Pretoria

Hänel, C. & Chown, S.L. (1998) The importance of a small, alien macro-invertebrate on a sub-Antarctic terrestrial ecosystem: *Limnophyes minimus* Meigen (Diptera, Chironomidae) at Marion Island. *Polar Biology* 20:99-106

Lewis Smith, R.I. (1990) Signy Island as a paradigm of biological and environmental change in Antarctic terrestrial ecosystems. In: Kerry, K.R. & Hempel, G. (eds) *Antarctic ecosystems. Ecological change and conservation*. Springer-Verlag, Berlin, pp. 32-50

Pugh, P.J.A. (1993) A synonymic catalogue of the Acari from Antarctica, the sub-Antarctic Islands and the Southern Ocean. *Journal of Natural History* 27:323-421

Simpson, R.D., Smith, S.D.A. & Pople, A.R. (1995) The effects of a spillage of diesel fuel on a rocky shore in the sub-Antarctic region (Macquarie Island). *Marine Pollution Bulletin* 31:367-371

Smith, F.A., Browning, H. & Shepherd, U.L. (1998) The influence of climate change on the body mass of woodrats Neotoma in an arid region of New Mexico, USA. *Ecography* 21:140-148