

Invertebrate body sizes from Marion Island

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Abstract: Body size was measured for 67 of the approximately 120 invertebrate species on Marion Island. These include more than 60% of the 29 acarine families, and more than 80% of the remaining terrestrial invertebrate species. Thus the data are regarded as representative of the entire invertebrate fauna of sub-Antarctic, Marion Island. Length–mass and fresh–dry mass relationships were calculated for orders, families and species to provide a means of estimating body size parameters for species in collections and those which are known from only a few specimens. A comparison of the regression slopes for the different taxonomic ranks indicates that it is better to use regressions from the lowest possible taxonomic level for prediction of body mass. Differences between length–mass relationships for Marion Island insects and continental assemblages raises the question as to the applicability of continental regressions to sub-Antarctic species. This study provides a useful means for estimating body size parameters for Antarctic and sub-Antarctic invertebrates and provides baseline data on an important species trait that seems to be changing with local and global environmental changes.

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Introduction

Body size is one of the most important characteristics of animals. Because it is correlated with many physiological and life history variables (Peters 1983), it may be used as a convenient indication of the likely value such traits (e.g. metabolic rate, fecundity) are to assume for a species of a given body size within a particular taxonomic group. Thus species body sizes are useful for providing a preliminary indication of the likely characteristics of a given set of species or assemblage (Gaston & Blackburn 2000). 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 (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 1999a), information on this important biological variable (and especially body mass) is not readily available, or at least not in a compiled format. Even where body length estimates are presented in the systematic literature, these usually assume the form of a size range, often ignoring gender- and age-related variation. 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 that

such compendia are being made available (Silva & Downing 1995), this constitutes an important lacuna in current knowledge regarding invertebrates, and particularly those of the broader Antarctic region.

Of course, this 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 parameter of body size from another (e.g. Miller 1976, Rogers *et al.* 1976, Smock 1980, Gowing & Recher 1984, Lang *et al.* 1997), 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 2000), 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 (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 (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 (e.g. Vernon & Voisin 1990, Davies *et al.* 1997, Convey & Smith 1997). The provision of such information from other areas should assist 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 2000). In addition, providing data on body sizes is essential because it also forms 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, Smith *et al.* 1998). Such change appears to be especially rapid in the Antarctic region (Bergstrom & Chown 1999, Smith 1990), providing a strong motivation for regular assessments of the body size of both particular species and whole assemblages in the region.

Here we 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 the majority of the insect,

spider, springtail, and mollusc 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.

Methods

Body size parameters (both mass and body length) were recorded from fresh specimens collected on Marion Island (46°54'S, 37°45'E) between 1986 and 1999. The majority of these measurements were recorded as part of the Marion Island Terrestrial Invertebrate Ecology programme (MITIE) between 1996 and 1999. For those species and stages which we were not able to sample sufficiently (e.g. *Pringleophaga marioni*) and for those families where previous studies have been quite extensive (e.g. the Curculionidae), we used the raw data collected by previous studies (Crafford 1990, Chown 1992, Chown & Crafford 1993, Klok & Chown 2001) that had been archived as part of the requirements within the South African National Antarctic Programme. Because these data were compiled from various sources they represent a suite of information collected over several years, during different

Table I. Mean fresh body mass (mg) and body length (mm) for Acari on Marion Island.

Order / Family	Species	Stage	Fresh mass (mg)			Body length (mm)			n
			mean ± s e	min	max	mean ± s e	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	<i>Macquariopppia striata</i> (Wallwork)	A	0.0416 ± 0.0060	0.0314	0.0550	0.62 ± 0.0217	0.57	0.67	4
Oppiidae	<i>Austropia crozetensis</i> (Richters)	A	0.0055 ± 0.0002	0.0048	0.0067	0.28 ± 0.0047	0.26	0.31	10
Oribatulidae	<i>Dometorina marionensis</i> van Plezten & Kok	A	0.0109 ± 0.0009	0.0058	0.0171	0.42 ± 0.0072	0.38	0.45	15
Ameronothridae	<i>Alaskozetes antarcticus intermedius</i> (Michael)	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
	<i>Halozetes belgicae</i> (Michael)	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
	<i>Halozetes fulvus</i> Englebrect	A	0.0314 ± 0.0009	0.0251	0.0409	0.62 ± 0.0044	0.58	0.67	22
	<i>Halozetes marinus</i> (Lohmann)	A	0.0948 ± 0.0017	0.0574	0.1302	—	—	—	58
	<i>Halozetes marionensis</i> Englebrect	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
	<i>Podacarus auberti</i> Grandjean	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
Prostigmata									
Nanorchestidae	<i>Nanorchestes</i> spp.	A/N	0.0005	—	—	0.14	0.14	0.14	3 (10)
Rhagidiidae	<i>Rhagidia</i> sp.	A/N	0.0180 ± 0.0005	0.0175	0.0185	0.61 ± 0.5952	0.62	0.01	2
Halacaridae	<i>Isobactrus magnus</i> (Lohmann)	A/N	0.0168 ± 0.0017	0.0044	0.0270	0.43 ± 0.0199	0.29	0.52	18
Ereynetidae	<i>Ereynetes</i> sp.	A/N	0.0007	—	—	0.17	—	—	1 (5)
Bdellidae	<i>Bdellodes</i> sp.	A/N	0.0522 ± 0.0170	0.0090	0.1552	0.66 ± 0.0886	0.33	1.12	8
Stigmaeidae	<i>Eryngiopis</i> sp.	A/N	0.0102 ± 0.0015	0.0018	0.0180	0.42 ± 0.0228	0.31	0.50	10
Erythreidae	<i>Balaustium</i> sp.	A	0.5206	—	—	1.643	—	—	1
Astigmata									
Hyadesiidae	<i>Hyadesia halophila</i> Fain	A/N	0.0131 ± 0.0010	0.0039	0.0265	0.39 ± 0.0111	0.26	0.50	26

Bracketed n denote the number of individuals weighed together to get a single mass. A = adults, N = nymphs, Lv = larvae, ∇ = naturalised aliens (the remaining species are taken to be indigenous).

seasons, and from different sites (but most usually on the east coast) on Marion Island. While we recognize that many species may show inter-annual (Block & Harrison 1995), site-related (Chown & Gaston 1999), and season related variation in body mass (Kari & Huey 2000), for the purpose of this paper we have assumed that this intraspecific variation is generally small compared to interspecific variation. Nonetheless, our results should be interpreted bearing these points in mind.

In those cases where new data were collected, a Mettler AE163 electronic microbalance (precision of 0.1 mg) was used to weigh the larger taxa (e.g. spiders, molluscs, earthworms and many of the insects) while a Mettler UMT2 electronic ultrabalance (precision of 0.1 µg) was used for the mites, springtails and smaller insects and life-stages. All measurements were taken from freshly collected material and all life-stages (e.g. adults, pupae, nymphs and larvae) were sampled where possible. Species-specific information with regard to the life-stages measured and sample sizes can be found in Tables I–III. All specimens were individually weighed with the exception of four taxa which were too small to weigh accurately: *Ereynetes* sp., where five individuals were weighed together (totalling 3.3 µg); *Nanorchestes* sp., where three groups of 10 individuals were weighed together (totalling 4.6 µg, 4.2 µg and 4.7 µg); *Megalothorax* sp., where 20 groups of five individuals were weighed together; and the Enchytraeidae where several individuals were weighed together (a similar approach has been used successfully by Block & Harrison 1995). A mean body mass was then calculated for each of the groups. Dry masses were calculated from specimens dried to constant mass for four days at 60°C. These results, although not given as means ± s.e., were used to calculate the fresh/dry mass relationships for selected taxa.

Linear dimensions were made using an ocular micrometer mounted in a Wild M3B dissecting microscope, and all measurements (except for the larger invertebrates) were made

at 40x magnification. For the mites, length was measured from the anterior tip of the gnathosoma to the posterior margin of the notogaster and the Collembola were measured from the anterior of the head to posterior of the abdomen. On the whole, insect length was measured from the anterior margin of the eye to final abdominal segment but for some taxa and life-stages other linear measures were employed and used as an indication of size. In the case of insect larvae, head capsules were measured at their widest point and for the spiders the length from the anterior to posterior margins of the cephalothorax were used as a reliable indication of overall linear dimensions. The linear measurement for the snail *Notodiscus hookeri* were measured across the widest diagonal of the shell from the lip of the shell aperture. More details on sample size and which linear measures were used can be found in Tables I–III. All body sizes were expressed in millimetres.

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). The length–mass 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.

Results and discussion

Body sizes were measured for 67 of the approximately 120 known invertebrate species found on Marion Island (see Crafford *et al.* 1986, Chown *et al.* 1998, Gabriel 1999, Marshall *et al.* 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 48 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

Table II. Mean fresh body mass (mg) and body length (mm) for the Collembola on Marion Island

Family	Species	Fresh mass (mg)				Body length (mm)			
		mean ± s.e.	min	max	n	mean ± s.e.	min	max	n
Neanuridae	<i>Friesea tilbrookii</i> Wise	0.1472 ± 0.0099	0.0750	0.2340	20	–	–	–	–
Hypogastruridae	<i>Ceratophysella denticulate</i> (Bagnall) [∇]	0.0201 ± 0.0025	0.0070	0.0520	20	1.08 ± 0.0463	0.74	1.39	20
	<i>Hypogastrura viatica</i> (Tullberg)	0.2862 ± 0.0409	0.1060	0.9870	20	2.37 ± 0.1269	1.67	3.80	20
Onychiuridae	<i>Tullbergia bisetosa</i> (Börner)	0.0882 ± 0.0094	0.0200	0.1540	20	1.31 ± 0.0571	0.93	1.85	20
Isotomidae	<i>Cryptopygus antarcticus travei</i> (Déharveng)	0.0441 ± 0.0054	0.0240	0.1140	20	2.15 ± 0.0879	1.60	2.87	20
	<i>Cryptopygus caecus</i> (Wahlgren)	0.0050 ± 0.0002	0.0040	0.0060	20	0.47 ± 0.0204	0.37	0.65	20
	<i>Cryptopygus dubius</i> (Déharveng)	0.0058 ± 0.0006	0.0030	0.0140	20	0.68 ± 0.0257	0.46	0.83	20
	<i>Cryptopygus tricuspus</i> (Enderlein)	0.0068 ± 0.0002	0.0060	0.0080	20	0.67 ± 0.0255	0.37	0.83	20
	<i>Isotoma marionensis</i> (Déharveng)	0.0128 ± 0.0007	0.0060	0.0200	20	1.54 ± 0.0290	1.39	1.85	20
	<i>Isotoma notabilis</i> (Schäffer) [∇]	0.0097 ± 0.0004	0.0070	0.0160	20	0.83 ± 0.0289	0.58	1.16	20
	<i>Isotomurus cf. palustris</i> (Müller) [∇]	0.0792 ± 0.0196	0.0100	0.4230	20	2.59 ± 0.0852	1.88	3.33	20
Tomoceridae	<i>Pogonognathellus flavescens</i> (Tullberg) [∇]	0.5088 ± 0.0824	0.1810	1.5330	20	2.96 ± 0.1376	2.03	4.06	20
Neelidae	<i>Megalothorax</i> sp. [∇]	0.0008 ± 0.0001	0.0004	0.0014	20 (5)	0.28 ± 0.0129	0.12	0.35	20
Sminthuridae	<i>Katianna</i> sp.	0.0256 ± 0.0028	0.0090	0.0620	20	0.56 ± 0.0394	0.37	1.01	20
	<i>Sminthurimus granulosus</i> Enderlein	0.0518 ± 0.0062	0.0270	0.1210	20	1.39 ± 0.0696	0.93	1.90	20
	<i>S. tuberculatus</i> Delamare Deboutteville and Massoud	0.0076 ± 0.0004	0.0040	0.0110	20	0.37 ± 0.0292	0.18	0.65	20

Bracketed *n* denote the number of individuals weighed together to get a single mass. ∇ = naturalised aliens (the remaining species are taken to be indigenous) (after Gabriel *et al.* in press).

records, transient aliens (Hänel *et al.* 1998, Hänel & Chown 1999b) 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 weights of taxa known from only a few specimens (e.g. Bartsch 1999).

Mean fresh body masses and body lengths (including head capsule widths, cephalothorax lengths and shell diameters) are provided for the Acari, Collembola, insects and other invertebrates in Tables I–III. Within each of the three major taxonomic groups, body mass spanned three orders of magnitude (Acari from 0.0005 to 0.5206 mg; Collembola from 0.0008 to 0.5088 mg; and adult insects from 0.03 to 26.17 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 and only selected taxa were measured. However, the

range does span two orders of magnitude, from 0.1 mm (*Nanorchestes* sp. - Table I) to over 10 mm for *Paractora dreuxi mirabilis* (Crafford *et al.* 1986).

For those taxa with sufficient data, length–mass regressions and fresh–dry mass regressions were calculated (Tables IV–VI). 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 ($\mu\text{g} = 10^{-6}\text{g}$). Both interspecific and intraspecific (insects only) regressions were positive and significant, and there were no outliers that warranted removal. Slopes of the intraspecific length–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. Thus, to broaden the applicability of these results, the regressions were extended to the family, order and class levels (Table V). Due to differences in slope of the relationships at the different levels (between families ANCOVA $P < 0.001$;

Table III. Mean fresh body mass and mean body length for the insects and other invertebrates on Marion Island. (continued opposite)

Order / Family	Species	Stage	Fresh mass (mg)				Body length (mm)			
			mean \pm s e	min	max	n	mean \pm s e	min	max	n
Psocoptera										
Elipsocidae	<i>Antarctopsocus jeanneli</i> Badonnel	A	0.4205 \pm 0.0282	0.1430	0.6320	23	–	–	–	–
Hemiptera										
Aphidoidea	<i>Rhaphalosiphum padi</i> (L.) [‡]	A?	0.2759 \pm 0.0200	0.0340	0.7000	64	0.98 \pm 0.2433	0.74	1.47	3
Thysanoptera										
Thripidae	<i>Apterothrips apteris</i> (Daniel) [‡]	A	0.0393 \pm 0.0017	0.0058	0.0640	40	1.11 \pm 0.0410	0.90	1.55	19
Coleoptera										
Hydraenidae	<i>Meropathus chuni</i> Enderlein [#]	A	0.5577 \pm 0.0264	0.4572	0.6916	10	2.24 \pm 0.0453	2.07	2.45	10
		Lv	0.1353 \pm 0.0224	0.0913	0.1642	3	1.63 \pm 0.1675	1.29	1.82	3
Staphylinidae	<i>Halmaeus atriceps</i> (C.O. Waterhouse) [#]	A	0.8002 \pm 0.0331	0.0610	1.4000	49	3.00	3.00	3.00	1
		P	0.4215	–	–	1	–	–	–	–
		Lv	0.4059 \pm 0.0234	0.0590	0.9000	59	3.48 \pm 0.1665	3.24	3.80	3
Curculionidae	<i>Bothrometopus parvulus</i> (C.O. Waterhouse) [#]	A	4.5441 \pm 0.1211	2.0400	8.7800	119	4.05 \pm 0.0689	3.53	4.59	22
	<i>Bothrometopus randi</i> Jeannel [#]	A	18.0877 \pm 0.7477	9.0100	36.1400	90	7.26 \pm 0.1553	5.66	8.36	22
	<i>Bothrometopus elongatus</i> (Jeannel) [#]	A	1.7149 \pm 0.0756	0.9700	12.4000	155	2.89 \pm 0.0337	2.47	3.29	45
		Lv	1.6629 \pm 0.4658	0.5360	5.1000	9	0.48 \pm 0.0269*	0.38*	0.60*	9
	<i>Ectemnorhinus</i> spp. [#]	A	16.8326 \pm 0.5588	1.9000	42.0500	235	6.18 \pm 0.0706	3.06	8.36	235
		P	24.8263 \pm 9.2165	6.6790	36.7000	3	7.75 \pm 0.0500	7.70	7.80	2
		Lv	5.7173 \pm 0.4883	0.1100	39.1000	209	0.64 \pm 0.0169*	0.24*	1.20*	209
	<i>Ectemnorhinus marioni</i> Jeannel	A	12.3286 \pm 0.5996	5.5100	24.5000	80	–	–	–	–
		Lv	7.7079 \pm 1.1813	0.1680	48.5000	62	0.60 \pm 0.0213*	0.26*	1.10*	102
	<i>Ectemnorhinus similis</i> Waterhouse	A	23.4954 \pm 0.8407	8.5000	41.1600	76	–	–	–	–
		Lv	7.3968 \pm 1.3860	0.0140	24.1000	28	0.66 \pm 0.0276*	0.29*	1.06*	61
	<i>Palirhoeus eatoni</i> (C.O. Waterhouse) [#]	A	7.3126 \pm 0.2105	4.2200	12.6800	90	4.54 \pm 0.0828	3.93	5.57	29
Diptera										
Physchodidae	<i>Pyschoda parthenogenetica</i> Tonnoir [‡]	A	0.2450 \pm 0.0981	0.0282	0.9000	8	–	–	–	–
		P	0.7000	–	–	1	–	–	–	–
		Lv	0.3790 \pm 0.1229	0.0554	0.9000	6	–	–	–	–
Chironomidae	<i>Telmatogeton amphibius</i> (Eaton) [#]	A	1.0843 \pm 0.1156	0.4370	2.6120	23	2.38 \pm 0.1457	1.65	4.63	23
		Lv	0.9864 \pm 0.1609	0.0100	5.0460	51	0.36 \pm 0.0220*	0.12*	0.62*	51
	<i>Limnophyes minimus</i> Meigen [‡]	A	0.1298 \pm 0.0155	0.0207	0.2286	18	–	–	–	–
		P	0.2468 \pm 0.0283	0.0431	0.5222	15	–	–	–	–
		Lv	0.2286 \pm 0.0166	0.0710	0.4077	34	0.17 \pm 0.0033*	0.17*	0.18*	3

= species used to calculate the insect length–mass regression, A = adults, P = pupae, Lv = larvae, Imm = immatures, * = headcapsule width (mm),

‡ = mean weights from variable number of individuals (1–40) weighed to get a single mass, † = naturalized aliens (the remaining species are taken to be indigenous) (after Hänel & Chown 1999b).

between orders ANCOVA $P = 0.0117$), we recommend that the regressions for the lowest possible rank in the taxonomic hierarchy still be used. While this point might appear to be self-evident, it should be noted that many previous studies of this nature have included a wide variety of species from several taxonomic groups (e.g. Rogers *et al.* 1976). Although such an approach is clearly useful in the absence of any alternative, it is important to note that results will be rather different as different levels within the taxonomic hierarchy are investigated. This point is similar to the one made by Chown & Gaston (1999) that there is no *a priori* reason why patterns at the intra- and interspecific levels should be similar or be explained by similar processes (see also Koslowki & Weiner 1997, Gaston & Blackburn 2000).

In the case of the mites the slopes of the interspecific length–mass regressions for the four orders (Mesostigmata, Cryptostigmata, Prostigmata and Astigmata) were not significantly different (ANCOVA, $P = 0.2141$). However, the elevations of the regressions were significantly different

(ANOVA, $P < 0.0001$), with significant differences between all the intercepts (Tukey HSD, $P < 0.0001$) except between the Astigmata and Prostigmata (Tukey HSD, $P = 0.9857$). While differences between the mite orders are to be expected given differences in their investment in integument, these differences were not always reflected in our analyses. This is clearly a consequence of the variance about the relationships, our choice of linear measurement (given that there is considerable shape variation within the mites – see Walter & Proctor 1999), and the taxa we were able to include in the analysis. Thus, in future investigations, it would be useful to know how general this apparent similarity of the slopes of the length–mass relationships for the mite orders is. At the interspecific level, and perhaps unsurprisingly, length–mass regressions for the Collembola, Acari and insects also had significantly different slopes (ANCOVA $P < 0.001$).

Rogers *et al.* (1976) found that for insects (excluding mites and springtails) the relationship between dry weight (W in mg) and length (L in mm) could be described by the equation

Table III. (continued) Mean fresh body mass and mean body length for the insects and other invertebrates on Marion Island.

Order/Family	Species	Stage	Fresh mass (mg)				Body length (mm)			
			mean \pm s.e.	min	max	n	mean \pm s.e.	min	max	n
Siaridae	<i>Lycoriella auberti</i> Séguy	A	0.0550 \pm 0.0041	0.0320	0.0950	22	–	–	–	–
Helcomyzidae	<i>Paractora dreuxi mirabilis</i> Séguy	A	12.2375 \pm 0.8395	4.2000	25.4000	40	–	–	–	–
		Lv	41.8186 \pm 0.7383	14.1000	94.2000	339	–	–	–	–
Tethinidae	<i>Listriomastax litorea</i> Enderlein	A	0.2253 \pm 0.0186	0.0800	0.3660	20	–	–	–	–
		Lv	1.9022 \pm 0.0866	0.1710	3.7000	66	2.75 \pm 0.3725	1.76	3.82	6
Drosophilidae	<i>Scaptomyza</i> sp. [‡]	A	3.5855 \pm 0.1635	1.4000	9.0000	69	–	–	–	–
		P	2.1333 \pm 0.2536	0.6000	3.3000	12	–	–	–	–
Fanniidae	<i>Fannia canicularis</i> (Linnaeus) [‡]	A	0.9000	–	–	1	–	–	–	–
Calliphoridae	<i>Calliphora vicina</i> Robineau-Desvoidy [‡]	A	1.7199 \pm 0.1321	0.5560	2.4030	21	–	–	–	–
		Lv	55.9160 \pm 4.1340	21.1000	101.2000	19	–	–	–	–
Lepidoptera	<i>Pringleophaga marioni</i> Viette	Lv	81.5330 \pm 4.1800	67.1000	106.9000	9	–	–	–	–
		A	26.1739 \pm 2.2546	11.0000	47.0000	18	–	–	–	–
		P	72.1667 \pm 9.5694	0.6000	146.7000	15	1.50 \pm 0.5271	0.49	2.26	3
Yponomeutidae	<i>Embryonopsis halticella</i> Eaton	Lv	23.8443 \pm 2.7929	0.2510	178.9000	141	1.32 \pm 0.1164	0.29	3.30	42
		A	3.8290 \pm 0.3550	2.1000	6.1000	14	–	–	–	–
		Lv	1.6520 \pm 0.2330	0.0740	14.7700	122	–	–	–	–
Hymenoptera	<i>Plutella xylostella</i> (Linnaeus) [‡]	A	9.7080 \pm 5.8920	1.9000	74.4000	12	–	–	–	–
		Lv	7.1540 \pm 0.6820	2.7000	11.9000	13	–	–	–	–
Eucoilidae	<i>Kleidotoma icarus</i> (Quinlan) [*]	A	0.3184 \pm 0.0236	0.1760	0.4900	13	1.98 \pm 0.0454	1.68	2.26	13
Arachnida	<i>Myro paucispinosus</i> Berland (high)	A	36.2069 \pm 8.0757	11.459	185.000	21	2.84 \pm 0.1337 [§]	2.03 [§]	4.00 [§]	20
		A	10.1752 \pm 2.1501	0.0444	57.200	32	–	–	–	–
		A	1.3422 \pm 0.0950	0.532	2.593	20	0.56 \pm 0.0280 [§]	0.289 [§]	0.863 [§]	20
		A?	0.639 \pm 0.0598	0.0223	3.4000	113	–	–	–	–
Gastropoda	<i>Notodiscus hookeri</i> Reeve	A	35.0143 \pm 2.7907	16.153	54.121	20	5.02 \pm 0.1654 ^Ø	3.62 ^Ø	6.08 ^Ø	20
		A	137.216 \pm 5.5869	103.973	185.118	20	–	–	–	–
Haplotaxida (Annelida)	<i>Deroceras caruanae</i> (Pollonera) [‡]	A	35.0143 \pm 2.7907	16.153	54.121	20	–	–	–	–
		A?	218.9 \pm 11.2	139.1	316.6	6	–	–	–	–
Lumbricidae	<i>Microscoclex</i> sp.	Imm?	24.300 \pm 1.700	1.0	76.3	14	–	–	–	–
		A/Imm	0.8423 \pm 0.0367	0.0785	2.68	20(¥)	–	–	–	–

= species used to calculate the insect length–mass regression, A = adults, P = pupae, Lv = larvae, Imm = immatures, * = headcapsule width (mm), § = cephalothorax length (mm), Ø = maximum shell diagonal (mm), ¥ = mean weights from variable number of individuals (1–40) weighed to get a single mass, ‡ = naturalized aliens (the remaining species are taken to be indigenous) (after Hänel & Chown 1999b).

Table IV. Intraspecific relationships between fresh mass and body length (or head capsule width) for selected insect species from Marion Island, with regression results.

Taxa	Stage	Equation	s e of intercept	s e of slope	s e of estimate	r^2	n	P
<i>Apterothrips apteris</i>	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			
<i>Meropathus chuni</i>	A	log M = -4.241 + 3.189 log x	0.3604	1.1480	0.3449	0.4909	10	0.0240
		log L = 0.805 + 0.154 log z	0.1838	0.0554	0.0758			
<i>Telmatogeton amphibius</i>	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			
<i>Telmatogeton amphibius</i>	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			
<i>Pringleophaga marioni</i>	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			
<i>Kleidotoma icarus</i>	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			
<i>Bothrometopus elongatus</i>	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			
<i>B. elongatus</i>	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			
<i>B. parvulus</i>	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			
<i>B. randi</i>	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			
<i>Ectemnorhinus</i> 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			
<i>Ectemnorhinus</i> 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			
<i>E. marioni</i>	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			
<i>E. similes</i>	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			
<i>Palirhoeus eatoni</i>	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			
<i>Notodiscus hookeri</i>	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			

A = adults, N = nymphs, Lv = larvae, M = mass (g), L = body length (mm), Hc = head capsule width (mm), Sd = shell diameter (mm), x = length (mm), y = head capsule width (mm), z = fresh mass (g), s = shell diameter (mm).

$W = 0.0305 \log L^{2.62}$ (or $\log W = 0.0305 + 2.620 \log L$). The slope of this relationship is significantly different from the slope of our insect length–mass equation ($\log M = -4.294 + 3.151 \log x$, Students t -test, $t = 20.38$, $P < 0.001$, 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) compared with this study. The latter authors examined species from 59 families and nine orders (weight range 0.02–800 mg, length range 0.5–36 mm), whereas we examined 11 insect species (i.e. excluding springtails and mites) from seven families and five orders (weight range 0.03–18 mg, length range 0.98–7.26 mm) (see Table III). This difference in the length–mass 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. Gowing & Recher (1984) found that there were no significant differences between the length–weight regressions of Australian and North American insects (comparing their equations to Rogers *et al.* 1976), concluding that this strengthens the value of generalized equations. However, because the families we 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 (Chown *et al.* 1998), in our view the present regression equations for insects should be used in preference to the one presented by Rogers *et al.* (1976).

Since most of the major springtail and mite taxa are represented in the Antarctic/sub-Antarctic, the regressions we have presented for these species should be considered more broadly applicable to other regions. We tested our mite length–fresh mass regression ($\log M_{\mu\text{g}} = 2.117 + 2.711 \log x$) against the length–dry mass regression described in Rogers *et al.* (1977) ($\ln M_{\mu\text{g}} = 3.682 + 2.761 \ln x$) and found no significant differences between the slopes of the two equations (Students t -test, $t = 0.3483$, $P = 0.7279$), substantiating the broader applicability of Rogers *et al.* (1977) results to the sub-Antarctic and the equations derived from our study to continental assemblages. However, we found highly significant differences between the elevations of the equations ($t = 447$, $P < 0.0001$). This is unsurprising considering that Rogers *et al.* (1977) used dry weights and natural logarithms to determine the regression.

Table V. Interspecific relationships between fresh mass and body length for selected mites, springtails, insects and spiders from Marion Island, with regression results.

Taxa	Stage	Equation	s e of intercept	s e of slope	s e of estimate	r ²	n	P
Acari (all spp.)	A/N/Lv	log M μ g = 2.117 + 2.711 log x log L = -0.760 + 0.354 log w	0.0104 0.0067	0.0333 0.0044	0.1053 0.0381	0.9595	281	< 0.0001
Astigmata	A/N/Lv	log M μ g = 2.143 + 2.550 log x log L = -0.799 + 0.354 log w	0.0719 0.0261	0.1714 0.0238	0.0563 0.0210	0.9022	26	< 0.0001
Cryptostigmata	A/N/Lv	log M μ g = 2.146 + 2.770 log x log L = -0.760 + 0.351 log w	0.0103 0.0072	0.0357 0.0045	0.0814 0.0289	0.9738	164	< 0.0001
Mesostigmata	A/N/Lv	log M μ g = 2.064 + 2.857 log x log L = -0.687 + 0.329 log w	0.0198 0.0212	0.1067 0.0123	0.9499 0.0322	0.9397	48	< 0.0001
Prostigmata	A/N/Lv	log M μ g = 2.124 + 2.808 log x log L = -0.733 + 0.335 log w	0.0467 0.0165	0.1107 0.0132	0.1505 0.0519	0.9401	43	< 0.0001
Collembola (all spp.)	A	log M μ g = 1.339 + 1.992 log x log L = -0.512 + 0.384 log w	0.0951 0.0900	0.3067 0.0591	0.3682 0.1616	0.7464	15	< 0.0001
Insects (all spp.)	A	log M = -4.294 + 3.151 log x log L = 1.343 + 0.309 log z	0.0179 0.0061	0.0262 0.0026	0.1225 0.0383	0.9719	421	< 0.0001
Curculionidae	A	log M = -4.1783 + 2.9977 log x log L = 1.3770 + 0.3252 log z	0.0190 0.0057	0.0258 0.0028	0.0651 0.0214	0.9747	352	< 0.0001
Coleoptera	A	log M = -4.1929 + 3.0160 log x log L = 1.3672 + 0.3203 log z	0.0217 0.0066	0.0298 0.0032	0.0857 0.0279	0.9659	363	< 0.0001
Spiders (all spp.)	A	log M = -2.415 + 1.838 log v log L.thx = 1.294 + 0.535 log z	0.0144 0.0262	0.0384 0.0112	0.0884 0.0477	0.9837	40	< 0.0001

A = adults, N = nymphs, Lv = larvae, M μ g = mass (μ g), M = mass (g), L = body length (mm), L.thx = cephalothorax length (mm), w = fresh mass (μ g), x = length (mm), z = fresh mass (g), v = cephalothorax length (mm).

In conclusion, although body size compilations are useful both from a macroecological perspective, and for estimating the likely nature of the physiology and life history characteristics of various species, such compilations remain relatively rare for invertebrates, and especially so for those from the broader Antarctic region. Indeed, few studies have included studies of a variety of higher taxa, making comparisons with faunas elsewhere problematic. For example, Walter & Behan-Pelletier's (1999) study concerned only mites, while the investigation undertaken by Morse *et al.* (1988) included only arboreal beetles. While there are apparently many compilations of insect body size data (see Gaston & Blackburn 2000) very few of them span several higher taxonomic groups, and this applies more broadly to body size studies in general. Thus it is only May (1978, 1986) who has made an explicit attempt to

determine the form of the body size frequency distribution across all taxa, and even this analysis had to be based on best estimates. In this study, we have taken a first step towards a comprehensive analysis of body size patterns at the assemblage level. What remains to be done are similar studies on continental faunas and other islands, as well as the inclusion of these data into a comprehensive analysis for all taxa on Marion Island. It seems likely that at least the former will be done for relatively species poor environments, while the latter is possible, at least in principle. Once such data are available, considerable insight should be possible into the effects that isolation and disharmony of the sub-Antarctic faunas (see Chown *et al.* 1998) have on the evolution of body size of the species constituting them.

Table VI. Relationship between fresh and dry body mass in selected taxa.

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

A = adults, P = pupae, L = larvae, Imm = immatures, M = fresh mass, Dm = dry mass, m = known dry mass (g), z = known fresh mass (g).

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