

Variation in size of living articulated brachiopods with latitude and depth

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Received: 21 January 2010 / Accepted: 28 May 2010 / Published online: 15 June 2010
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Abstract Geographical variations in animal characters are one of the main subjects for study in macroecology. Variation with latitude has received special interest. Articulated brachiopods are possibly the commonest macrofossil with large variations in size of taxa through the fossil record. Here, we investigate trends in size of the 3 main orders of articulated brachiopod with latitude and depth. Data were insufficient to identify patterns in Thecideida (a micromorph taxon only recorded from low latitudes). Rhynchonellida had no clear trends in size with latitude or depth. Terebratulida exhibited hemispheric differences in size relations, with increasing length of species towards the pole in the south and no significant trend in the north. Tropical species were small (<20 mm length between 10°N and 10°S), and the largest species were found between 30° and 60° latitude in both hemispheres. There were no articulated brachiopods recorded from the high arctic, and support for a continuous trend in size with latitude was small or absent. In Terebratulida, there was a significant decrease in species

length with depth of 1.7 mm per 100 m depth increase. These trends could be explained by competition for space and reduced availability of habitat with progressive depth beyond the continental shelf.

Introduction

Geographic patterns of size variation in animals have been of interest to biologists for decades. Much of the effort in the field of macroecology is aimed at understanding how characteristics such as size, distribution and abundance of organisms vary at large spatial and temporal scales (e.g. Gaston and Blackburn 2000). One of the most prominent theories concerning variation in body size is that of Bergmann's rule that states that "within a species the body mass increases with latitude and colder climate, or that within closely related species that differ only in relation to size that one would expect the larger species to be found at the higher latitude" (Bergmann 1847). The rule is most commonly applied to endotherms, and indeed was originally formulated for warm blooded animals. There have also been many examples of patterns that would fit Bergmann's rule in ectotherms (e.g. Partridge and French 1996; Chappelle and Peck 1999; Ashton 2004); however, there have been several authors arguing strongly against a universal rule of this type (e.g. Geist 1987), and trends of size increase in the opposite direction have been documented (e.g. Nylin and Svärd 1991). Also organisms living at higher latitude or altitude are usually longer lived and slower growing (Peck et al. 2006), and achieving larger size while having slower growth rates is counter intuitive. Most life history models also predict smaller size at maturity in environments that reduce growth rates (see Berrigan and Charnov 1994). Despite this, such patterns of increase in

Communicated by X. Irigoien.

Electronic supplementary material The online version of this article (doi:10.1007/s00227-010-1486-5) contains supplementary material, which is available to authorized users.

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size with latitude and altitude on land are widely accepted and much effort has been put into explaining them (e.g. Angilletta 2004, Chown and Gaston 2009). Explanations include different temperature effects on growth and differentiation (van der Have and de Jong 1996), oxygen availability constraints on cell size (Woods 1999; Chapelle and Peck 1999, 2004, Peck and Chapelle 2003; Peck and Maddrell 2005), energy use (Brown et al. 2004), abundance (White et al. 2007), diet quality (Ho et al. 2010), geographic range size or through increased fecundity or survival in cold environments (Stearns 1992). The various explanations are reviewed in Angilletta (2004), but there is still no consensus and either different factors are important in different groups or multiple factors interact to give the effect.

Investigations of trends in size in animals are dominated by studies of latitudinal effects. However, other factors have been shown to be important, including resource availability, where large size confers an advantage through reduced mass specific costs with increasing size, or shorter seasons reduce capacity to attain large size (e.g. Schutze and Clarke 2008); altitude (e.g. Ma et al. 2009); oxygen availability (Chapelle and Peck 1999; Peck and Maddrell 2004; McClain and Rex 2001); and in the sea, with depth (Rex and Etter 2009). The latter is of interest, because several factors change with increasing depth, including resource availability and suitable habitat for hard substratum dwelling species. Trends of increasing size towards abyssal depths have been well documented for gastropod molluscs (Rex et al. 1999). However, other taxa show different outcomes with either decreasing size or no trend with depth (Rex and Etter 2009). Most of these have, however, been studies of infauna or mobile taxa, and studies of species living attached to rock surfaces are rare.

Articulated brachiopods have existed on Earth for over 500 million years since the Early Cambrian. There are examples in the fossil record of very large articulated brachiopods, in particular some strophomenates during Carboniferous and Permian, and they are one of the groups that support the idea that over evolutionary time clades tend to evolve towards larger size (Cope's rule) (Novack-Gottshall 2008). This rule has received criticism with respect to sampling bias (Jablonski 1996), but such trends are still well accepted. Trends in size of living articulated brachiopods could be instructive in understanding size trends with latitude or depth in the sea in deep time but such studies are scarce or absent. The largest living brachiopod *Magellania venosa* grows to over 90 mm and lives in cool temperate southern latitudes at sites, for example around Chile and the Falkland Islands. This suggests there may be latitudinal trends in articulated brachiopod size that would match predictions from Bergmann's rule. The aim of this study was

to identify if such trends exist in the extant articulated brachiopod clades.

Methods

Two methods were used to collect data on size of brachiopods used in this investigation. Firstly, large samples of brachiopods collected from 15 sites around the world were examined in detail to identify the largest specimens of any articulated brachiopod species present. These sites were as follows: Signy Island and the Weddell Sea in Antarctica, Chile, The Falkland Islands, 5 sites in New Zealand (Doubtfull Sound, Otago Harbour, Otago Shelf, Antipodes Islands, and samples labelled NZ waters from McQuarie Island, Chatham Island and Campbell Island), 6 sites in Australia (Western Port Bay, Victoria, SW of Cape Adieu, South Australia, Port Jackson, NSW, Swain Reefs, GBR, Middleton Reef, Tasman Sea, Oyster Bay, Tasmania). The samples from sites in New Zealand were made available by NIWA, and those for Australia by the Australian Museum. In total, 24 collections were evaluated and 4,521 specimens measured using vernier calipers (± 0.1 mm). For each of these sites, the length of the largest individual of any species present was noted. These data were then combined with all published length data for extant articulated brachiopods that we were able to identify and access. This amounted to 68 published sources including papers and monographs.

For each species measured, we additionally recorded the following information: membership of the order they belong to, collection location, latitude (to the nearest 0.5°) and the depth range of the collection (in metres).

In our analyses, we opted to use minimum depths where samples were collected over a range of depth. Although this may in some cases underestimate the depths at which a taxon was collected (for example those sampled using a dredge from a ship, and where the dredge sample was collected over a varying depth range), it is preferable to analysing size trends based on minimum depth because of the possibility of transport down slope (we know of no mechanism that might have caused movement in the reverse direction). Depth data were divided into three bins at <200 , $200\text{--}1,000$ and $>1,000$ m. These were aimed at representing the continental shelf, slope and deep water habitats. Latitudinal analyses were performed on data also split into bins, and the size of bin chosen was the smallest that contained enough data in each bin to allow analyses to be performed. Sixteen data sources were rejected because authors did not record depths sampled. Where a published report amalgamated measurements from stations in the same general location, we recorded the lower latitude. All of the above data are presented in electronic supplementary material. Of the

75 genera of terebratulide listed in the *Treatise on Invertebrate Paleontology* (Lee et al. 2006), we have data from 71 (95%), and of these 71 genera all except 4 are represented in our data set by the type species. Of the 17 genera of rhynchonellide listed in the *Treatise* (Savage et al. 2002), we have data from 15 (i.e. 88%) and type species data for 10 of them. Of the 5 genera of thecideid listed, in either the latest *Treatise* (Baker 2006) or described subsequently, we have data from 4 and quote type species data for 2 of these.

In our analyses, to avoid bias, data were limited to one entry per species. Where data were available for a species for more than one site or depth the data used for latitude and depth were for the largest size quoted.

Results

Length data with the latitude and depth data for the site sampled are given in electronic supplementary material (Appendix a). Data for terebratulides were analysed separately from those for rhynchonellides or thecideids.

Terebratulida

When maximum size for all terebratulide species studied are plotted against latitude the pattern that appears is one of two clusters of brachiopods, with only small species inhabiting tropical latitudes between 5°N and 5°S (Fig. 1), and a dearth of specimens sampled from the Arctic (only one record for latitudes beyond 60°N). One species *Magellania venosa* is apparent for being much larger than any other terebratulide, attaining a length beyond 90 mm, compared to the 62.5 mm for the next largest species. The variation in size with latitude can be analysed by splitting the data into 10° latitude bins, and testing for differences between bins. When this is done, there is no significant variation in size of terebratulide brachiopods with latitude for the overall data (ANOVA, $F = 1.29$, 14,248 *df*, $P = 0.22$).

Following this analysis, data were separated into three depth categories: species with minimum depth records shallower than 200 m; species with minimum depth records between 200 and 1,000 m; and species with minimum depth records beyond 1,000 m. When the shallowest species (continental shelf, min depth < 200 m) are considered, the dearth of large specimens in the tropics is even more apparent. The largest species recorded from these latitudes *Frenulina cruenta* (Cooper 1973) is 17.8 mm in length. There is a complete absence of records for terebratulide species from the Arctic in the 0–200 m depth range. In both hemispheres, species attaining lengths beyond 50 mm only occur at latitudes beyond 35°. There appears to be a pattern of increasing size with latitude in both hemispheres. How-

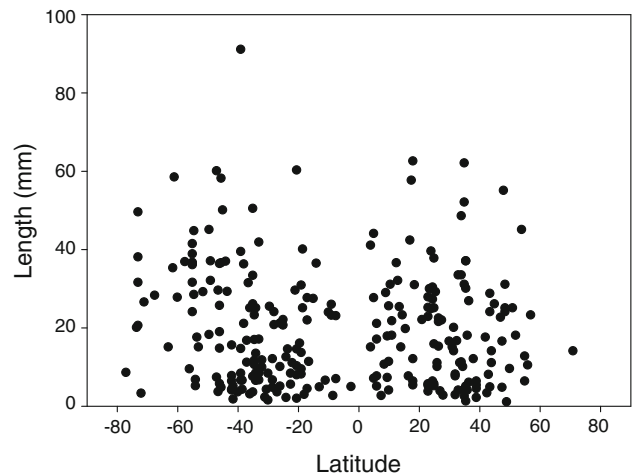


Fig. 1 Distributions of terebratulide brachiopod species with latitude and length. Each data point represents a single species for the maximum size either measured in this study or quoted in the literature plotted against the latitude where the sample was taken. There is only one entry per species and where multiple records are available only the site where the largest specimen occurred is quoted. All available data for terebratulide species are quoted

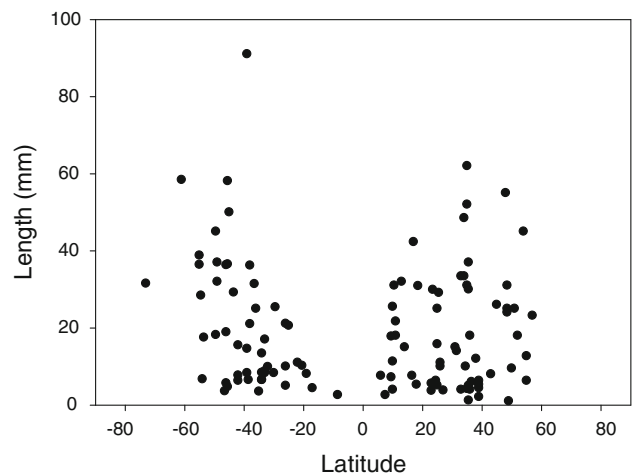


Fig. 2 Distributions of length data versus latitude for terebratulide brachiopods reported living at depths shallower than 200 m. Only one entry per species is quoted and where multiple records are available only the site where the largest specimen occurred is quoted

ever, when this trend is tested by dividing the data into 20° latitude blocks the trend in the Southern Hemisphere is significant (ANOVA for Southern Hemisphere: $F = 3.40$, 3,48 *df*, $P = 0.025$), but the Northern Hemisphere has no significant variation (ANOVA for Northern Hemisphere: $F = 0.58$, 3,61 *df*, $P = 0.63$) (Fig. 2). Regressions of size versus latitude (where size is measured as length in mm, latitude is in degrees) produce a similar result (Southern Hemisphere: $Lth = -4.69 - 0.654Lat$, $r^2 = 0.2$, $F = 11.9$, $n = 51$, $P < 0.001$; Northern Hemisphere: $Lth = 14.2 + 0.132Lat$, $r^2 = 0.016$, $F = 0.99$, $n = 64$, $P = 0.32$).

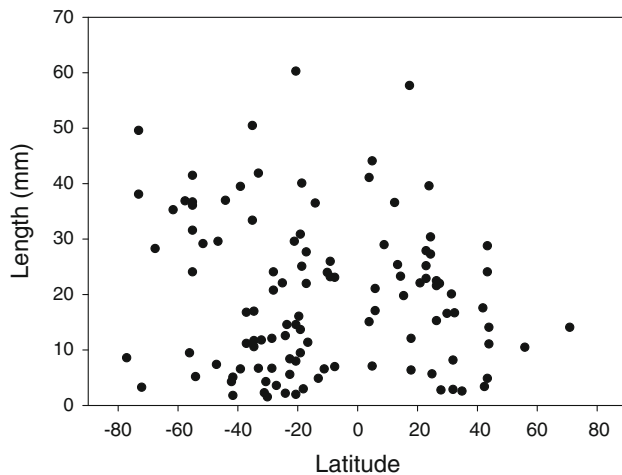


Fig. 3 Distributions of length data versus latitude for terebratulide brachiopods reported living at depths between 200 and 1,000 m. Only one entry per species is quoted and where multiple records are available only the site where the largest specimen occurred is quoted

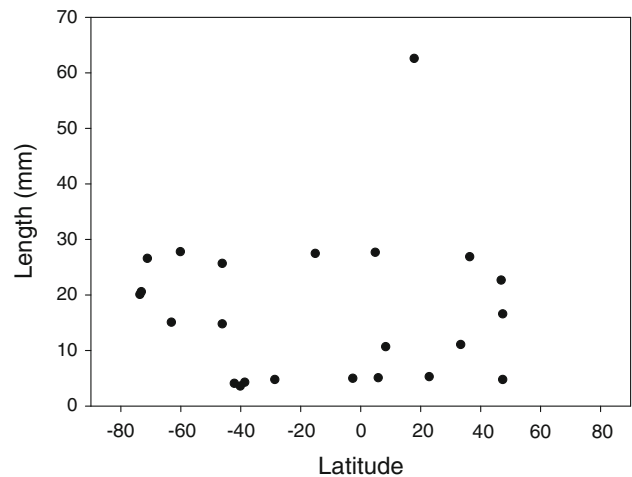


Fig. 4 Distributions of length data versus latitude for terebratulide brachiopods reported living at depths deeper than 1,000 m. Only one entry per species is quoted and where multiple records are available only the site where the largest specimen occurred is quoted

When species with shallowest recorded occurrence is between 200 and 1,000 m depth are considered the pattern obtained is very different from that for shallow (continental shelf) species (Fig. 3). Similarities include that the distribution includes some large species over 50 mm in length and records for northern high latitudes are very sparse, with only 2 species living further then 50°N. However, records for species living between 10°N and 10°S include several species over 20 mm length, and some species over 40 mm length (Fig. 3). In contrast to data for species from shallower than 200 m depth there is no significant trend in length with latitude in the Southern Hemisphere ($L_{th} = 13.6 - 0.172Lat$, $r^2 = 0.031$, $F = 0.32$, $n = 69$, $P = 0.08$), but there is a significant decrease in length with latitude in the Northern Hemisphere ($L_{th} = 25.5 - 0.247Lat$, $r^2 = 0.071$, $F = 0.42$, $n = 44$, $P = 0.04$). It should be noted that the low number of samples from northern high latitudes may have affected this result, as the species recorded from 71°N (*Arctosia arctica* (Friele, 1878)) had a strong residual effect on the regression.

Species living beyond 1,000 m depth were small, being less than 30 mm in length with the exception of one species (*Dyscolia wyvilli*) which attained a length of 62 mm (Fig. 4). There were no significant trends in size for terebratulide species living deeper than 1,000 m in either the Southern ($L_{th} = 6.31 - 0.196Lat$, $r^2 = 0.11$, $F = 2.51$, $n = 12$, $P = 0.14$) or Northern Hemisphere ($L_{th} = 22.5 - 0.119Lat$, $r^2 = 0.01$, $F = 0.11$, $n = 9$, $P = 0.74$). There is also no clear lack of larger specimens at tropical latitudes, although the data are limited.

The reduction in maximum size with depth becomes more apparent when size of species from all latitudes is plotted against depth, where no species larger than 30 mm

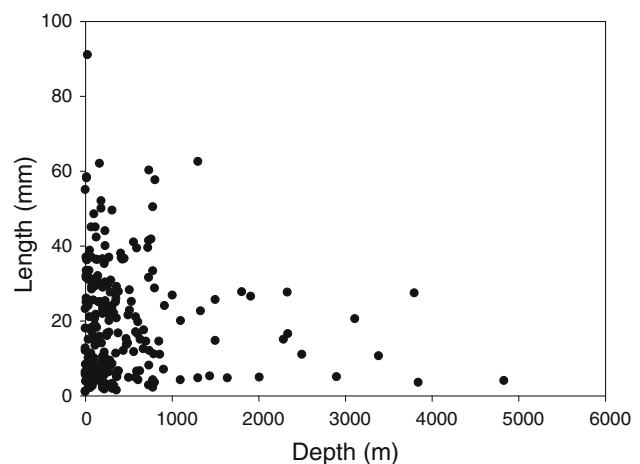


Fig. 5 Length data for terebratulide brachiopods plotted against depth. Only one entry per species is quoted and where multiple records are available only the depth where the largest specimen occurred is quoted

length have been recorded deeper than 1,500 m (Fig. 5). When these data are separated into 500 m depth bins and the length of the largest specimen in each bin regressed with depth a significant relationship is obtained, where the length of the largest species in a depth horizon declines on average by 1.7 mm for every 100 m of depth increase ($L_{th} = 76.1 - 0.0166Depth$, $r^2 = 0.68$, $F = 18.2$, $n = 8$, $P = 0.004$).

Rhynchonellida and Thecideida

Rhynchonellide brachiopods grow to smaller sizes than terebratulides. Only one species attains a length beyond 28 mm and that is *Neorhynchia strebeli* that grows to

57 mm at a depth of over 2,500 m of New Caledonia (24°S) (Laurin 1997). There are also far fewer rhynchonellide species in the World's oceans than terebratulides. Thus, patterns of size distribution will not be as easy to identify. When data for Rhynchonellida are plotted against latitude for each of the depth horizons previously studied (0–200, 200–1,000, and >1,000 m), there are no trends in size in either hemisphere for any depth range (Fig. 6). There is also no clear indication of a lack of larger specimens in the lowest latitudes (10°N to 10°S) in the shallowest depth range as seen in the terebratulides. Interestingly there is a lack of specimens in shallow sites (<200 m depth) at high latitude, beyond 50° in either hemisphere. In both of the deeper depth horizons there are rhynchonellides sampled from high latitude in the Southern Hemisphere, but not the North. Also, unlike the data for terebratulides, there is no trend in size with depth (data not shown).

Thecideid brachiopods are very small. The maximum lengths reported in the literature for species of this group range from 2.1 mm (*Thecidellina minuta* (Cooper, 1981)) to 8.4 mm (*Thecidellina maxilla* (Hedley, 1899)). This group is also not often reported, and size data were only available for 10 species (supplementary electronic material: Appendix a). It was not possible to split these species for analysis in depth horizons. When all species sampled are analysed against latitude, species from low latitudes (22.5°S to 10°N) ranged from 4.9 to 8.8 mm length ($n = 7$), and were all larger than any specimen collected from higher latitudes ($n = 3$, range 2.1–3.4 mm). When thecideid size is considered with depth, only small species occur deeper than 200 m depth, but again the sample size is small and the trend non-significant ($Lth = 6.37 - 0.00815Depth$, $r^2 = 0.26$, $F = 4.08$, $n = 10$, $P = 0.08$, where Lth is in mm and depth in m). The lack of species sampled from high latitudes seen in the terebratulides and rhynchonellides is even more extreme in the thecideids, where we have been unable to find records of any species from latitudes higher than 44° in either hemisphere.

Discussion

Biogeography and depth distributions

Articulated brachiopods have often been described as a group inhabiting fiords, caves, polar regions and the deep sea (Rudwick 1970; Curry et al. 1989; James et al. 1992; Peck 2001). The data here indicate that this is not true for thecideids, because there are no records of them in high latitudes, beyond 44° in either hemisphere. Rhynchonellide species do occur at high latitudes, but not at depths shallower than 200 m, and they have only been recorded at high latitude in the Southern Hemisphere. Terebratulides also

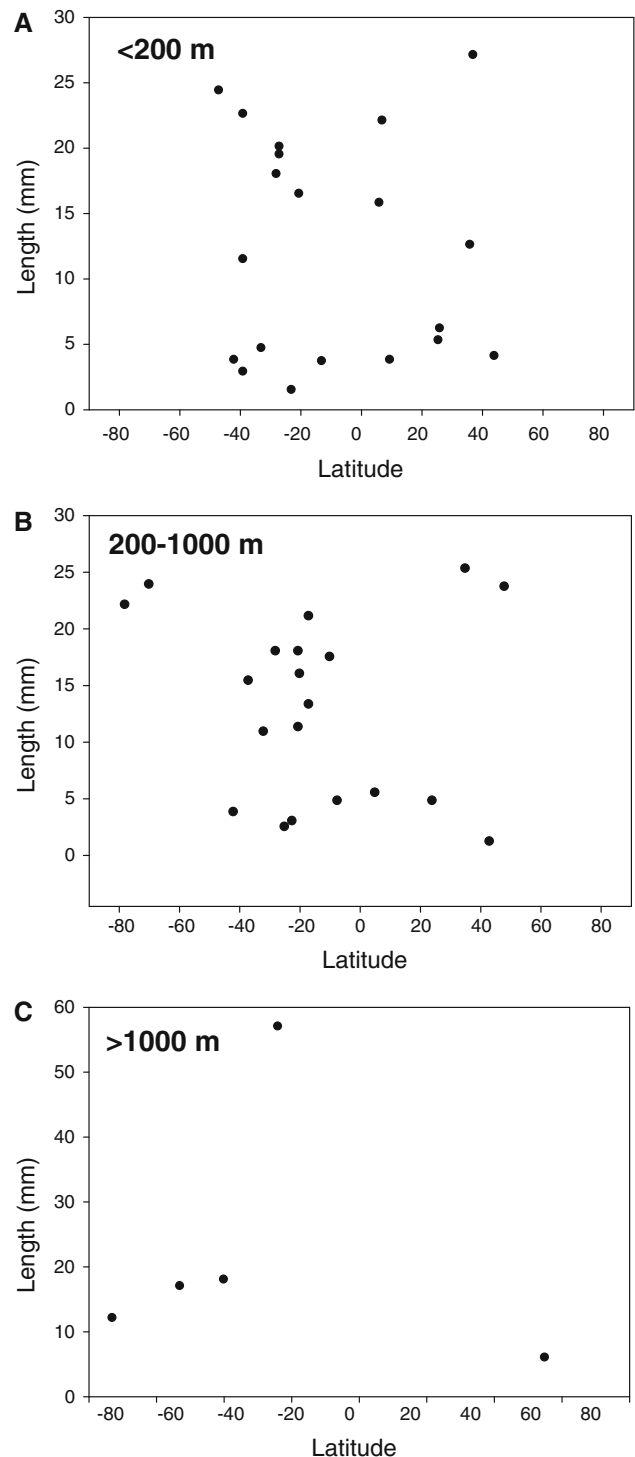


Fig. 6 Distributions of length data versus latitude for rhynchonellide brachiopods reported living at depths: **a** Shallower than 200 m; **b** between 200 and 1,000 m; and **c** deeper than 1,000 m. Only one entry per species is quoted and where multiple records are available only the site where the largest specimen occurred is quoted

occur at high latitudes in the Southern Hemisphere, but only one species has been recorded beyond 58° in northern latitudes. These 3 main articulated brachiopod groups are,

therefore, essentially absent from northern high latitude sites in the Arctic. Zezina (2008) also noted an absence of articulated brachiopods in the Arctic.

The lack of articulated brachiopods in the Arctic is an example of a difference in biodiversity pattern between the hemispheres. Such differences have been identified previously in animal characteristics such as cold hardiness in insects (Sinclair et al. 2003). They are also evident in snowlines, treelines, frost tolerance of trees, and proportions of winter deciduous species (Woodward 1987; Körner 1998; Körner and Paulsen 2004). The reasons for these differences are still yet to be characterised. However, Chown et al. (2004) have argued that the mechanisms proposed to explain diversity gradients can be reduced to three categories: historical, ecological or null. Zezina (2008) argued that a major factor in setting current articulated brachiopod latitudinal diversity patterns is historical. However, the absence of articulated brachiopods in the Arctic is difficult to explain in that context, and more work is needed to elucidate which, or which combination of the three mechanisms identified by Chown et al. (2004) is important here.

Zezina (2008) showed that the number of brachiopod species present in the World's oceans varies with depth, that the depth horizon with the most species is between 100 and 200 m depth, and that numbers of species then decline with further depth. Our data would tend to corroborate these findings, as there were fewer species per 100 m of depth in the 200–1000 m category (17.1 species 100^{-1} m depth) than the less than 200 m depth category (77.5 species 100^{-1} m depth). Numbers of species were even lower in the deepest category, >1,000 m (1.0 species 100^{-1} m depth). Although there are data showing that numbers of species per unit depth declines from the continental shelf progressively to deeper sites, there are problems with this analysis. The numbers of samples collected and the areas sampled decline markedly with depth, and this factor will automatically cause a reduction of numbers per unit depth at deeper sites. There is also a reduction in available habitat with depth for species that live attached to a rock substratum such as articulated brachiopods. Because of this reduction in available habitat the reductions in numbers of species with depth seen here and reported by Zezina (2008) probably do reflect a reduction in species numbers with depth.

Overall, therefore, the categorisation of articulated brachiopods being species of caves, fiords, deep sea and the polar regions needs revision. They are species of the deeper continental shelf and upper slope, that when occurring in shallow sites can often be found in high densities in caves, fiords and the Antarctic (e.g. Forsterra et al. 2008).

Size variation with latitude and depth

The size distribution data for extant Thecideida are insufficient to allow an analysis of trends with either latitude or depth. That species recorded from low latitudes are all larger than those from mid or high latitudes and that shallow species were larger than deep cannot be verified as trends with latitude or depth because only 10 species have been recorded for size worldwide. This group is, however, comprised of only very small species, the largest *Thecidellina maxilla* only reaching a maximum recorded length of 8.8 mm. Rhynchonellida do not show significant trends in size with either latitude or depth. Again sample numbers are small, and this may explain the lack of trends. There are, however, several elements of the size distributions of terebratulids that are of interest. The lack of large specimens in the 10°N to 10°S latitudinal range is not easy to explain. There is significant hard substratum habitat in this region, including several tropical reefs. However, species recorded here are generally micromorph. It may be that grazing pressure restricts species to genuinely cryptic habitats and hence restricts maximum size, as suggested by Asgaard and Stentoft (1984) and Asgaard and Bromley (1991). However, reports that articulated brachiopod tissues contain chemical defences (e.g. McClintock et al. 1993; Mahon et al. 2003) and the tissues of articulated brachiopods are so low in energy that cost to benefit analyses indicate predators should preferentially take bivalve molluscs (Peck 1993) would argue against this. Alternative explanations hinge on factors such as space competition from algae and other attached invertebrates. However, tropical articulated brachiopods are often found in cryptic habitats such as caves where such competition is low (e.g. Thayer and Allmon 1991). The reason for the small size of articulated brachiopods in this zone is, therefore, still obscure but presumably all these hypotheses hinge on exclusion to refuges where life is generally less fast, less dangerous.

The trends with latitude seen in Terebratulida here are most evident in the shallowest depth range investigated, where a significant increase in size with latitude is present in the Southern Hemisphere, but not the Northern Hemisphere. This may be an unexpected result. There are, however, very few studies analysing trends with latitude in separate hemispheres, even using the simple technique here of dividing data into 20° bins (Chown et al. 2004). There are studies that have shown different patterns of organism characteristics in the two hemispheres, including a range of insect physiological attributes (Chown et al. 2004), upper survival temperatures in marine algae (Wiencke et al. 1994), and temperature tolerances in marine invertebrates (Richard, pers. comm.). The differences in pattern here raise several unanswered questions including: why are

articulated brachiopods not recorded from the Arctic? Why are brachiopods in shallow depths at the lowest latitudes predominantly micromorph? And why are there no species of terebratulide brachiopod living in the shallowest 200 m larger than 10 mm length in the southern tropical region, whereas several species at these latitudes in the north attain lengths beyond 20 mm.

There are significant differences in several physical environmental factors in the two hemispheres. 70% of the land mass is in the Northern Hemisphere, oceanic circulation patterns at high latitude are predominantly north-south in the Northern Hemisphere and west-east in the Southern Hemisphere, and around 90% of the world's ice is in the southern polar region. The difference in the amount of land mass in the two hemispheres may also be a factor in the different hemispheric trends in size seen here, because the areas of continental shelf available for colonisation are smaller in the Southern Hemisphere. This means that available habitat is less, with a concomitant restraint on factors such as range size. However, this difference in available area should also affect the deeper ranges studied here, where no latitudinal trends were seen, and hence the environmental characters dictating this trend must be stronger in the <200 m depth range. Environmental characters specific to this depth horizon include light, space competition with benthic algae and predation. More work is needed to identify the intensity of effects of such characters on brachiopods across latitudes.

Chown et al. (2004) stated that “comparisons of latitudinal gradients and their underlying correlates in the two hemispheres for the same taxon, sampled using similar methods, and investigated with methods that take cognisance of likely confounding effects are required”, especially in relation to predicting likely biota responses to climate change. Brachiopod life history characters of slow growth, brooding, and low metabolic rates have been suggested as factors making them more vulnerable in changing environments (Peck 2008). Studies like the present are therefore needed to identify how patterns in different taxa vary in large regional scale to help identify characters of importance in predicting resistance to environmental change.

Studies of trends in size with depth in marine ectotherms are rare. There are examples of both dwarfism (e.g. Tietjen 1989), or gigantism in the deep sea (e.g. La Perna 2005). McClain et al. (2006) compared size relations between deep sea and shallow water molluscs. They did this to test the island biogeography size hypothesis that there is a graded trend from gigantism in small-bodied species to dwarfism in large-bodied species. They argued that the deep sea has characters in common with islands that may make this phenomenon present in deep versus shallow comparisons. These include low absolute food

availability. They found that genera of gastropods with small body size in shallow water tend to large body size at depth and vice versa. They concluded that controls of maximum size attained are through resource constraints, seen through food supply. Our data for terebratulides shows a clear trend of decreasing size with depth. This could be support for the idea of resource limitation controls of size with depth. However, articulated brachiopods are recognised as a low energy group, where shallow species have amongst the lowest metabolic rates of any invertebrate measured (e.g. James et al. 1992), and very small abilities to raise their metabolism (Peck 1996). They also have slow growth (Peck et al. 1997), and very slow development rates (Peck and Robinson 1994; Peck et al. 2001). These are characters that should give brachiopods advantages in low food availability environments, and hence an increase in size with depth on the island hypothesis may be expected.

As with latitude, differences between hemispheres, available habitat for obligatory hard substratum attached species declines on the continental slope and onto deep and abyssal depths. Thus, the maximum numbers of species of articulated brachiopod reported at depths of 150–200 m by Zezina (2008), and the decline in size with depth may be due to a combination of factors. Competitive exclusion may limit habitat availability in the photic zone, and reduced habitat availability may constrain articulated brachiopods at depth. This would result in both profiles seen.

Overall, in the order where sufficient samples are available to identify trends, Terebratulida, hemispheric trends in size with latitude are different, with an increase in length at higher latitudes at shallow depths in the south and no significant trend in the north. In both hemispheres there is support for Bergmann's rule at low latitudes, as size increases with latitude. At mid depths (200–1,000 m) there is no trend in the south, but a decrease in size with latitude in the Northern Hemisphere. However, in both hemispheres the largest species occur at mid-latitudes between 30° and 60°, and size decreases with latitude thereafter. This trend is much clearer in the north where brachiopods are essentially absent from the Arctic. Thus, there is little support for Bergmann's rule overall in this study, and ecological factors (competition, predation, resource availability, etc.) probably dictate sizes seen. In the terebratulides size also decreases significantly with depth, and this trend is clearer than trends with latitude. These patterns with depth may also reflect effects of constraints due to competition and habitat availability.

Acknowledgments We thank Ian Loch for loan of Australian Museum specimens and NIWA for the loan of specimens from cruises and sites around New Zealand.

References

- Angilletta MJ Jr (2004) Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integr Comp Biol* 44:498–509
- Asgaard U, Bromley RG (1991) Colonisation by micromorph brachiopods in the shallow subtidal of the eastern Mediterranean Sea. In: MacKinnon DI, Lee DE, Campbell JD (eds) *Brachiopods through time*. A.A. Balkema, Rotterdam, pp 261–264
- Asgaard U, Stenfort N (1984) Micromorph brachiopods from Barbados: palaeoecological and evolutionary implications. *Geobios Memoire Special* 8:29–37
- Ashton KG (2004) Sensitivity of intraspecific latitudinal clines of body size for tetrapods to sampling, latitude and body size. *Integr Comp Biol* 44:403–412
- Baker PG (2006) Thecideida. In: Kaesler RL (ed) *Treatise on Invertebrate Paleontology, Part H Brachiopoda*, Revised, vol 5. The Geological Society of America and The University of Kansas, Boulder & Lawrence, pp 1938–1964
- Bergmann C (1847) Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien* 3(1):595–708
- Berrigan D, Charnov EL (1994) Reaction norms for age and size at maturity in response to temperature: a puzzle for life historians. *Oikos* 70:474–478
- Brown JH, Gillooly JF, Allen AP, Savage V, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85:1771–1789
- Chapelle G, Peck LS (1999) Polar gigantism dictated by oxygen availability. *Nature* 399:114–115
- Chapelle G, Peck LS (2004) Amphipod crustacean size spectra: new insights in the relationship between size and oxygen. *Oikos* 106:167–175
- Chown SL, Gaston KJ (2009) Body size variation in insects: a macroecological perspective. *Biol Rev*. doi:10.1111/j.1469-185X.2009.00097.x
- Chown SL, Sinclair BJ, Leinaas HP, Gaston KJ (2004) Hemispheric Asymmetries in Biodiversity—A Serious Matter for Ecology. *PLoS Biol* 2(11):e406. doi:10.1371/journal.pbio.0020406
- Cooper GA (1973) New Brachiopoda from the Indian Ocean. *Smithsonian Contrib Paleobiol* 17:1–51
- Cooper GA (1981) Brachiopoda from the Southern Indian Ocean (recent). *Smithsonian Contrib Paleobiol* 43:1–93
- Curry GB, Peck LS, Ansell AD, James M (1989) Physiological constraints on living and fossil brachiopods. *Trans R Soc Edinb Earth Sci* 80:255–262
- Forsterra G, Hausserman V, Lüter C (2008) Mass occurrence of the recent brachiopod *Magellania venosa* (Terebratulidae) in the fiords Comau and Renihue, Northern Patagonia, Chile. *Mar Ecol Evol Perspect* 29:342–347
- Gaston KJ, Blackburn TM (2000) *Pattern and process in macroecology*. Blackwell Science, Oxford
- Geist V (1987) Bergmann's rule is invalid. *Can J Zool* 65(4):1035–1038
- Hedley C (1899) Mollusca of Funafuti, part 2, Pelecypoda and Brachiopoda. *Memoirs Austr Museum* 3:508–510
- Ho CK, Pennings SC, Carefoot TH (2010) Is diet quality an overlooked mechanism for Bergmann's rule? *Am Nat* 175:269–276
- Jablonski D (1996) Body size and macroevolution. In: Jablonski D, Erwin DH, Lipps J (eds) *Evolutionary paleobiology*. University of Chicago Press, Chicago, pp 256–289
- James MA, Ansell AD, Collins MJ, Curry GB, Peck LS, Rhodes MC (1992) Recent advances in the study of living brachiopods. *Adv Mar Biol Rev* 28:175–387
- Körner C (1998) A re-assessment of high elevation treeline positions and their explanation. *Oecologia* 115:445–459
- Körner C, Paulsen J (2004) A world-wide study of high altitude treeline temperatures. *J Biogeog* 31:713–732
- La Perna R (2005) A gigantic deep-sea Nucinellidae from the tropical West Pacific (Bivalvia : Protobranchia). *Zootaxa* 881:1–10
- Laurin B (1997) Brachiopodes récoltées dans les eaux de la Nouvelle-Calédonie et des îles Loyauté, Matthew et Chesterfield. In: Crosnier A (ed) *Résultats des campagnes MUSORSTOM*, vol 18. *Mémoires Museum Natl Hist Nat* 176:411–471
- Lee DE, Smirnova TN, Dong-Li S (2006) Terebratulida. In: Kaesler RL (ed) *Treatise on Invertebrate Paleontology, Part H Brachiopoda*, Revised, Volume 5. The Geological Society of America and The University of Kansas, Boulder & Lawrence, pp 1965–2250
- Ma X, Lu X, Meril J (2009) Altitudinal decline of body size in a Tibetan frog. *J Zool* 279:364–371
- Mahon AR, Amsler CD, McClintock JB, Amsler AO, Baker BJ (2003) Tissue-specific palatability and chemical defenses against macro-predators and pathogens in the common articulate brachiopod *Liothyrella uva* from the Antarctic Peninsula. *J Exp Mar Biol Ecol* 290:197–210
- McClain CR, Rex MA (2001) The relationship between dissolved oxygen concentration and maximum size in deep-sea turrid gastropods: an application of quantile regression. *Mar Biol* 139:681–685
- McClain CR, Boyer AG, Rosenberg G (2006) The island rule and the evolution of body size in the deep sea. *J Biogeog* 33:1578–1584
- McClintock JB, Slattery M, Thayer CW (1993) Energy content and chemical defence of the articulate brachiopod *Liothyrella uva* (Jackson, 1912) from the Antarctic Peninsula. *J Exp Mar Biol Ecol* 169:103–116
- Novack-Gottshall PM (2008) Ecosystem-wide body-size trends in Cambrian-Devonian marine invertebrate lineages. *Paleobiology* 34:210–228
- Nylin S, Svärd L (1991) Latitudinal patterns in the size of European butterflies. *Holarctic Ecology* 14:192–202
- Partridge L, French V (1996) Thermal evolution of ectotherm body size: why get big in the cold? In: Johnston IA, Bennet AF (eds) *Animals and temperature: phenotypic and evolutionary adaptation*. Cambridge University Press, Cambridge, pp 265–292
- Peck LS (1993) The tissues of articulate brachiopods and their value to predators. *Philos Trans R Soc Lond B* 339:17–32
- Peck LS (1996) Feeding and metabolism in the Antarctic brachiopod *Liothyrella uva*: a low energy lifestyle species with restricted metabolic scope. *Proc R Soc Lond B* 263:223–228
- Peck LS (2001) Ecology. Chapter 11. In: Carlson S, Sandy M (eds) *Brachiopods ancient and modern: a tribute to G. Arthur Cooper*. The Paleontology Society of the USA & the University of Kansas, USA, pp 171–183
- Peck LS (2008) Brachiopods and climate change. *Earth Environ Sci Trans R Soc Edinburgh* 98:451–456
- Peck LS, Chapelle G (2003) Reduced oxygen at high altitude limits maximum size. *Proc R Soc Lond BL* 270:S166–S167
- Peck LS, Maddrell SHP (2005) The limitation of size by oxygen in the fruit fly *Drosophila melanogaster*. *J Exp Zool* 303A:968–975
- Peck LS, Robinson K (1994) Pelagic larval development in the brooding Antarctic brachiopod *Liothyrella uva*. *Mar Biol* 120:279–286
- Peck LS, Brockington S, Brey T (1997) Growth and metabolism in the Antarctic brachiopod *Liothyrella uva*. *Philos Trans R Soc Lond Ser B* 352:851–858
- Peck LS, Meidlinger K, Tyler PA (2001) Developmental and settlement characteristics of the Antarctic brachiopod *Liothyrella uva* (Broderip 1833). In: Brunton CHC, Cocks LR, Long SL (eds) *Brachiopods past and present. The systematic association special volume series 63*, London, pp 80–90
- Peck LS, Convey P, Barnes DKA (2006) Environmental constraints on life histories in Antarctic ecosystems: tempos, timings and predictability. *Biol Rev* 81:75–109
- Rex MA, Etter RJ (2009) *Deep-sea biodiversity: pattern and scale*. Harvard University Press, London, 332 pp

- Rex MA, Etter RJ, Clain AJ, Hill MS (1999) Bathymetric patterns of body size in deep-sea gastropods. *Evolution* 53:1298–1301
- Rudwick MJ (1970) Living and fossil brachiopods. Hutchinson University Library, London
- Savage NM, Manceñido MO, Owen EF, Carlson SJ, Grant RE, Dagens AS, Sun DL (2002) Rhynchonellida, 1027–1376. In: Kaesler RL (ed) Treatise on invertebrate paleontology. Part H. Brachiopoda 4 (revised). Geological Society of America, Boulder, CO, and University of Kansas Press, Lawrence, KS, 753 pp
- Schutze MK, Clarke AR (2008) Converse Bergmann cline in a Eucalyptus herbivore, *Paropsis atomaria* Olivier (Coleoptera: Chrysomelidae): phenotypic plasticity or local adaptation? *Glob Ecol Biogeogr* 17:424–431
- Sinclair BJ, Addo-Bediako A, Chown SL (2003) Climatic variability and the evolution of insect freeze tolerance. *Biol Rev* 78:181–195
- Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford
- Thayer CW, Allmon RA (1991) Unpalatable thecideid brachiopods from Palau—ecological and evolutionary implications. In: MacKinnon DI, Lee DE, Campbell JD (eds) Brachiopods through time. A.A. Balkema, Rotterdam, pp 253–260
- Tietjen JH (1989) Ecology of deep-sea nematodes from the Puerto Rico Trench area and Hatteras Abyssal Plain. *Deep-Sea Res* 36:1579–1594
- Van der Have TM, de Jong G (1996) Adult size in ectotherms: temperature effects on growth and differentiation. *J Theor Biol* 183:329–340
- White EP, Ernest SKM, Kerkhoff AJ, Enquist BJ (2007) Relationships between body size and abundance in ecology. *TREE* 22:323–330
- Wiencke C, Bartsch I, Bischoff B, Peters AF, Breeman AM (1994) Temperature requirements and biogeography of Antarctic, Arctic and Amphiequatorial seaweeds. *Bot Mar* 37:247–259
- Woods HA (1999) Egg-mass size and cell size: effects of temperature on oxygen distribution. *Am Zool* 39:244–252
- Woodward FI (1987) Climate and plant distribution. Cambridge University Press, Cambridge, 174 p
- Zezina ON (2008) Biogeography of the Recent Brachiopods. *Paleontol J* 42:830–858