

Latitudinal gradients in body size in marine tardigrades

PAUL J. BARTELS^{1*}, DIEGO FONTANETO², MILENA ROSZKOWSKA^{3,4},
DIANE R. NELSON⁵ and ŁUKASZ KACZMAREK³

¹*Department of Biology, Warren Wilson College, Asheville, NC 28815, USA*

²*Consiglio Nazionale delle Ricerche, di Ricerca Sulle Acque CNR-IRSA, Verbania Pallanza, Italy*

³*Department of Animal Taxonomy and Ecology, Adam Mickiewicz University, Poznan, Uniwersytetu Poznańskiego 6, 61-614 Poznań, Poland*

⁴*Department of Bioenergetics, Adam Mickiewicz University, Poznan, Uniwersytetu Poznańskiego 6, 61-614 Poznań, Poland*

⁵*Department of Biological Sciences, East Tennessee State University, Johnson City, TN 37614, USA*

Received 20 October 2018; revised 3 July 2019; accepted for publication 27 July 2019

Homeotherms and many poikilotherms display a positive relationship between body size and latitude, but this has rarely been investigated in microscopic animals. We analysed all published records of marine Tardigrada to address whether microscopic marine invertebrates have similar ecogeographical patterns to macroscopic animals. The data were analysed using spatially explicit generalized least squares models and linear models. We looked for latitudinal patterns in body size and species richness, testing for sampling bias and phylogenetic constraints. No latitudinal pattern was detected for species richness, and sampling bias was the strongest correlate of species richness. A hump-shaped increase in median body size with latitude was found, and the effect remained significant for the Northern Hemisphere but not for the Southern. The most significant effect supporting the latitudinal gradient was on minimum body size, with smaller species disappearing at higher latitudes. Our results suggest that biogeographical signals were observed for body size, albeit difficult to detect in poorly studied groups because of swamping from biased sampling effort and from low sample size. We did not find a significant correlation with the latitudinal pattern of body size and ecologically relevant net primary productivity.

ADDITIONAL KEYWORDS: Bergmann's rule – size–latitude relationship – ecogeographical rules – everything is everywhere – net primary productivity – species richness – Tardigrada – water bears.

INTRODUCTION

Body size is the ‘single most important axis of biodiversity’ (Brown *et al.*, 2007), with profound impacts on everything from basic cellular processes to global biogeographical patterns (Hildrew *et al.*, 2007). The surface area-to-volume ratio decreases with cell or body size, and this shapes many of the differences between micro- and macroorganisms (Peters, 1983; Schmidt-Nielsen, 1984; Brown *et al.*, 2007).

Body size at the community level is affected by environmental gradients at different spatial scales, from the local scale, sometimes associated with potential anthropogenic pressures (e.g. Lefort *et al.*, 2015; Merckx *et al.*, 2018), to the large scale, sometimes

associated with natural biogeographical clines (e.g. Hillebrand, 2004; Watt *et al.*, 2010). Latitudinal gradients of diversity have been said to be unlikely in most microorganisms (Hillebrand & Azovsky, 2001; Fenchel & Finlay, 2004; Azovsky & Mazei, 2013) owing to their widespread distribution (Fenchel & Finlay, 2004; de Wit & Bouvier, 2006; Fontaneto, 2011). Yet, not all microorganisms have cosmopolitan distributions, and many do show some degree of endemism (for a broad summary, see Foissner, 1999, 2006; Fontaneto, 2011; Faurby & Barber, 2015; Garraffoni & Balsamo, 2017). In addition, even if dispersal is perhaps easy for microscopic animals (Fontaneto, 2019), species-specific differences in habitat suitability might be correlated with geographical gradients and produce latitudinal patterns of diversity, especially if some mechanisms governing body size are correlated with latitude.

*Corresponding author. E-mail: pbartels@warren-wilson.edu

Latitudinal trends in community-level body size have received renewed interest in recent years owing to potential impacts of global climate change (Gardner *et al.*, 2011; Rasconi *et al.*, 2015; Sommer *et al.*, 2017; Zohary *et al.*, 2017). The main mechanisms that have been suggested to drive community-level large-scale latitudinal gradients in body size are Bergmann's rule (Bergmann, 1847) and the resource availability hypothesis (Huston & Wolverton, 2011). Bergmann's rule is the classic and well-studied trend towards larger body size at higher latitudes in animals for which heat conservation correlates to size-related differences in surface-to-volume ratios (Blackburn *et al.*, 1999; Daufresne *et al.*, 2009). The long and rich history of the description of latitudinal gradients in body size according to Bergmann's rule is summarized by Watt *et al.* (2010), with a table listing 23 different definitions that have been invoked (see also Meiri, 2011). The resource availability hypothesis suggests that large body size is often adaptive for multiple reasons, but is constrained by resource availability. If resources are correlated with latitude, this could drive differences in body size.

Despite the attention focused on describing patterns in body size–latitude relationships since the mid-19th century, they have rarely been studied in microscopic animals. Microscopic animals are similar in size to most unicellular eukaryotes, but they are true multicellular animals, with complex organ systems. We define microscopic animals as those < 2 mm in adult body length, because this is the number most frequently given for the cosmopolitan transition. These are predominantly benthic meiofauna, although a few micro- or mesozooplankton species also fall into this size range. Intraspecific patterns of increased body size with decreased rearing temperatures are known in some microscopic animals (Forster *et al.*, 2012), but we know of only a few reports of interspecific differences in body size with latitude in small animals. One example is in monogeneans, which are aquatic ectoparasitic helminths < 1 cm long (Poulin, 1996), for which, at the family level, a positive but non-significant correlation was found between body size and latitude (Poulin, 1996). Another example is in the marine tardigrade genus *Echiniscoides*, for which a gradient in body size was noticed between European locations, although no statistical support was offered (Kristensen & Hallas, 1980).

Tardigrades (phylum Tardigrada), commonly called water bears, are free-living animals consisting of > 1300 species and subspecies (Guidetti & Bertolani, 2005; Degma & Guidetti, 2007; Degma *et al.*, 2009–2018; Vicente & Bertolani, 2013). They are microscopic invertebrates, usually ranging in body length from 75 to 1200 µm (Fig. 1). They are ubiquitous, living in freshwater, marine and terrestrial habitats worldwide.

Terrestrial tardigrades live in the aquatic film around moss, lichens and soil, and they are famous for their ability to undergo cryptobiosis to withstand periods of drying, freezing and other environmental extremes (Ramazzotti & Maucci, 1983; McInnes, 1994; Nelson *et al.*, 2015). However, this capability is not observed in most of the aquatic taxa (but see Kristensen & Hallas, 1980; Clausen *et al.*, 2014; Jørgensen & Møbjerg, 2014). Marine water bears are part of the meiobenthos (Giere, 2019) and, like most meiobenthic animals, they have direct development, lacking a planktonic stage (Warwick, 2007). For a summary of their biology, see Kinchin (1994) and Nelson *et al.* (2015).

There are > 200 species and subspecies of marine tardigrades, a fraction of the almost 1100 known from terrestrial and freshwater habitats (Guidetti & Bertolani, 2005; Degma & Guidetti, 2007; Degma *et al.*, 2009–2018; Bartels *et al.*, 2016), largely attributable to low investigative effort (Bartels *et al.*, 2016; Fontoura *et al.*, 2017). They inhabit marine sediments or are associated with algae or larger invertebrates, and are generally smaller than limnoterrestrial tardigrades, averaging ~200 µm maximum body length. A recent comprehensive literature review (Kaczmarek *et al.*, 2015) listed all published records of marine tardigrades, and these data provided the basis for the present analyses. Marine tardigrades are ideal model microscopic animals for biogeographical studies. They are well below the presumed cosmopolitan transition size, they occur from the Arctic to the Antarctic, and ocean currents could potentially provide global connectivity. However, they lack planktonic larvae, and population sizes are usually low (Giere, 2013).

Here, we explore whether these microscopic animals have any biogeographical structure regarding latitudinal gradients in species diversity and body size. We then examine whether such patterns can be driven by habitat productivity, the most plausible mechanism for microscopic poikilotherms.

MATERIAL AND METHODS

OCCURRENCE DATA

A database was compiled of all records of marine tardigrades ever published in peer-reviewed literature from 1865 to the end of 2014 by Kaczmarek *et al.* (2015), and only records identified to species level were included. However, we also corrected errors and omissions and added all new records of marine tardigrades published in 2015 and 2016. Nomenclature was updated based on the checklist by Degma *et al.* (2009–2018, 33rd edition) in order to avoid using more synonyms for the same taxonomic unit. We also compiled body sizes for each species. Body size ranges were determined based on

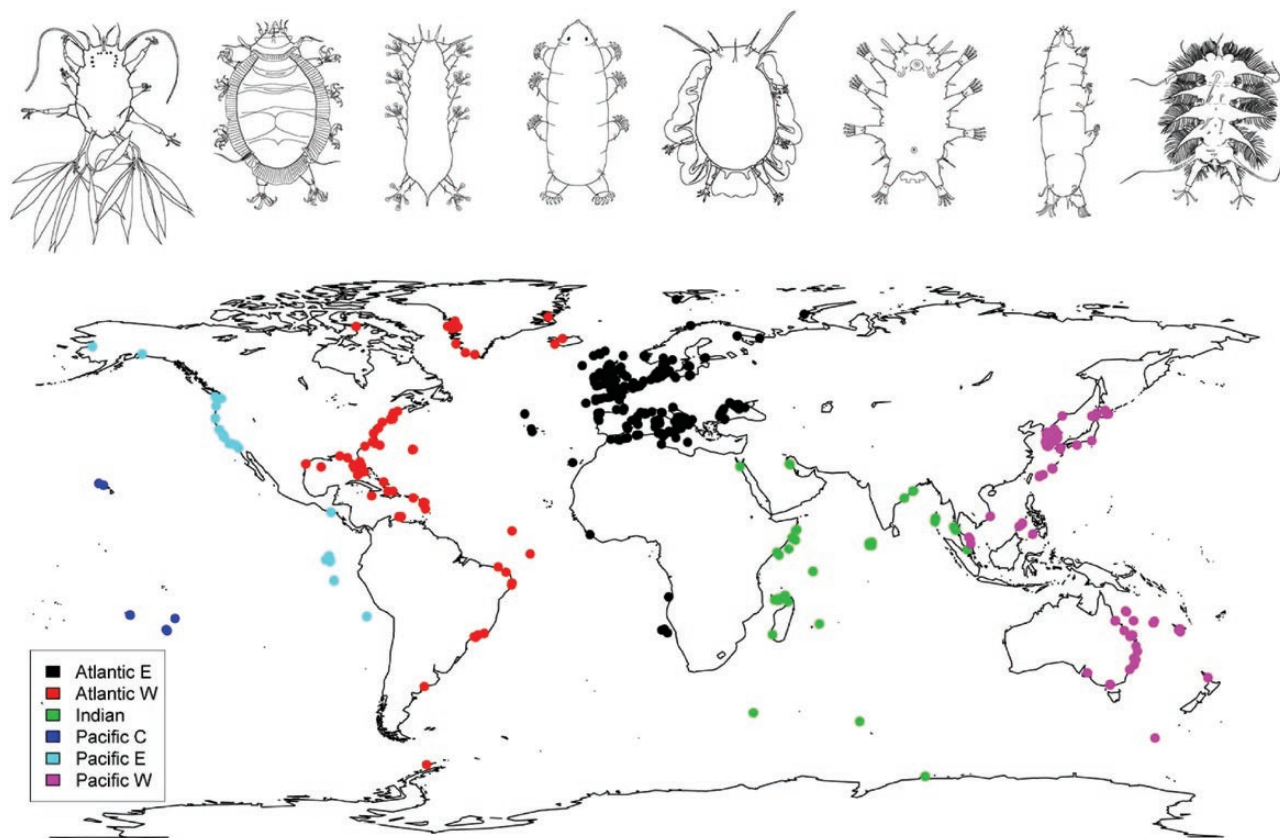


Figure 1. Map of the world, with all occurrence records divided into the six main areas. Drawings at the top illustrate some of the diversity of marine tardigrades: from left to right, *Zioella*, *Parmursa*, *Batillipes*, *Echiniscoides*, *Florarctus*, *Mutaparadoxipus*, *Coronarctus* and *Neostygarctus*. Drawings are modified from Fontoura *et al.* (2017).

original descriptions or redescrptions of adult females of each species. The maximum size reported was recorded for each species, given that tardigrades grow with each moult throughout their lives (Nelson *et al.*, 2015; Altiero *et al.*, 2018). Each record in the database includes the name of the species, its taxonomic position, the paper reporting the finding and the coordinates of the locality. The bibliographic survey contained 332 papers that included occurrence data. The final dataset included 2340 occurrence records from 209 species or subspecies belonging to 50 genera, 14 families, three orders and two classes covering the entire world (Fig. 1). This low number of records makes identification of a biogeographical signal difficult, but we suggest that if a pattern is seen in such a small sample size, the pattern must be strong. Genus abbreviations follow Perry *et al.* (2019).

GEOGRAPHICAL UNITS

The dataset had single point records from all over the world. In order to assess the relationship between

diversity and latitude, we grouped the occurrence data in geographical units represented by grids of 1° latitude and longitude. In addition, we repeated the analyses using occurrence data from larger square grids of 2, 5 and 10° latitude and longitude, to confirm the generality of the observed patterns.

Moreover, given that most records come from sediments on continental slopes and could be connected physically along the edges of continents, we grouped the geographical units at all spatial scales into the following six large homogeneous areas corresponding to connected coastal areas: West Atlantic Ocean, East Atlantic Ocean, Indian Ocean, West Pacific Ocean, Central Pacific Ocean and East Pacific Ocean (Fig. 1). We acknowledge that such gross subdivision might be questionable; nevertheless, it represents a reliable way to group geographical units according to their geographical proximity and connectivity along continental slopes. The area of the Central Pacific Ocean was not defined by proximity to continents, but precisely by its remoteness from any continental margin.

VARIABLES

Our main aim was to explore the latitudinal gradients in community-level body size in marine tardigrades. For each latitudinal grid, we measured various metrics summarizing body size, i.e. the median, minimum and maximum body size of all the species found in each grid. Each of these metrics might reveal different facets of differences in body size across latitudinal gradients. Differences in latitudinal gradients between the three metrics could provide insights into the potential correlates of the pattern. For example, even in the absence of differences in median values, the overall effect of latitude could be to reduce maximum body size or to increase minimum body size.

Various confounding factors might be responsible for an apparent gradient in body size, including biased knowledge of species richness and sampling bias. To minimize the effect of such biases, we measured some potential confounding factors explicitly and included them in our statistical models. The variables that we measured for each geographical unit grid were the species richness, number of occurrence records and number of published papers to account for sampling bias.

STATISTICAL MODELS

Before fitting any model on latitudinal gradients in body size, we explored whether latitudinal gradients in species richness existed or if sampling bias could be a much stronger correlate of our understanding of biological diversity in such an understudied group of organisms as marine tardigrades. The first set of models explored the effect of latitude on species richness at different spatial scales, using measurements from grids at 1° (and at 2, 5 and 10°, with results reported in the [Supporting Information Table S1, S2, S3](#)). Although these grids have a different area correlating with latitude, we did not correct our analyses for such bias; few records are available at higher latitudes, and no records at all are known above 80°, where the effect would be more apparent. In addition, grid area would not be the best predictor for available surface given that most samples come from coastal areas, and different grids of the same area might still have a completely different surface occupied by coastal areas. An additional reason not to include grid area in the models is that it is highly correlated with latitude, and the effect of two highly correlated variables in the same model would cancel each other out, not fulfilling the assumptions of any statistical test ([Crawley, 2012](#)). Thus, we did not correct our models for analysed area, but we consider that the effect of sampling bias and latitudinal gradients should not be affected by grid area. Latitude was entered with its absolute and its squared values to test for linear and hump-shaped

relationships. Additional potential confounding factors entered into the models were the number of records and the number of papers, accounting for sampling bias and unequal biogeographical knowledge. Variables represented by count data (i.e. species richness, number of records, number of papers) were \log_{10} -transformed to account for the fact that they span up to three orders of magnitude and have a geometric behaviour ([Crawley, 2012](#)). Moreover, all explanatory continuous variables, after \log_{10} -transformation in the case of count data, were scaled before running statistical models to remove the effect of differences in scale and sampling units between variables ([Zuur et al., 2009](#)). Given the large number of statistical models fitted on the same dataset, we used a strictly cautionary approach to identify significance and assumed a restrictive α -level of 0.001 instead of the more common α -level of 0.05.

For each analysis, we assessed whether a significant spatial structure was present by performing generalized least squares (GLS) models fitted by maximizing log-likelihood. With the use of GLS, we could test different shapes of potential spatial correlation patterns, including exponential, Gaussian, linear, rational quadratic and spherical correlation structure ([Zuur et al., 2009](#)), on the same statistical models. We used the Akaike information criterion (AIC) to select the best model among the non-spatial and spatial ones, with all the different correlation structures for each set of models. Model fits through likelihood ratio tests on AIC were used to indicate whether the spatial models were significantly better than the non-spatial ones. In cases with no improvement attributable to the inclusion of a spatial structure, we used the results of linear models (LMs) with the same structure as the corresponding GLS model, because they are simpler in their interpretation. All analyses were performed in R v.3.1.2 ([R Core Team, 2014](#)) and GLS with the package *nlme* v.3.1-118 ([Pinheiro et al., 2014](#)).

For each final model, either an LM with no spatial structure or a GLS model with spatial structure, we provided the output according to a type II ANOVA table using the R package *car* ([Fox & Weisberg, 2011](#)). For LMs, we also included partial R^2 for each explanatory variable, estimated as the averaged contribution over orderings among explanatory variables ([Chevan & Sutherland, 1991](#)). Moreover, for both LMs and GLS models, we estimated the relative importance (RI) value of each explanatory variable by model averaging ([Burnham & Anderson, 2002](#)). This was calculated, on a scale from zero to one, as the sum of the Akaike weights of the submodels in which the variable appeared, from the set of submodels including all combinations of explanatory variables. A variable that contributed more to model fit would have a higher RI value, closer to one.

We performed all the steps of the analyses on latitudinal gradients in species richness including the division into the six main geographical areas (West Atlantic Ocean, East Atlantic Ocean, Indian Ocean, West Pacific Ocean, Central Pacific Ocean and East Pacific Ocean; Fig. 1) as an additional confounding factor.

The same structure of the analyses, with \log_{10} -transformation, scaling, testing for spatial autocorrelation structure, GLS models and LMs, partial R^2 and model averaging, was applied to analyse latitudinal gradients in body size. The explanatory variables in the models were the absolute and quadratic values of latitude, subdivision into six areas and richness as a potentially confounding factor. The response variables were different metrics of body size, i.e. median, minimum and maximum body length for each species assemblage of each grid. Moreover, we repeated the analyses including only data from the Northern and from the Southern Hemisphere to check for differential drivers of latitudinal gradients between the two hemispheres.

A potential confounding factor that would be difficult to include in the models on latitudinal gradients is attributable to phylogenetic constraints in geographical distribution and also in body size. For example, body size could be constrained phylogenetically, and species in the same biogeographical area might have a common origin, artefactually connecting latitude with body sizes. We explored the effect of these constraints using phylogenetic comparative methods (Garamszegi, 2014). The phylogenetic relationships we used to address the phylogenetic effect were derived from the most recently published papers addressing the topic (Fujimoto *et al.*, 2016; Møbjerg *et al.*, 2016) and from the established taxonomy of the phylum (Degma *et al.*, 2009–2018). Given the possibility of a phylogenetic signal (Munkemüller *et al.*, 2012) in the comparisons between different species in the dataset, we tested whether our data were phylogenetically structured using Pagel's λ (Pagel, 1999) and Blomberg's K (Blomberg *et al.*, 2003). Values of Pagel's λ and Blomberg's K close to zero indicate a lack of phylogenetic signal, which occurs when closely related species are not more similar than distantly related ones. Values closer to one indicate that closely related species are significantly more similar than expected by chance (Kamilar & Cooper, 2013). We tested whether there was a phylogenetic signal in the minimum, maximum and median values of latitude and on the overall latitudinal range for each species, using latitudinal values as both actual and absolute values. Moreover, we also tested whether there was a phylogenetic signal in body size and in the number of records for each species, given that larger species might be detected more easily than small ones.

We then used phylogenetic generalized least squares (PGLS) analyses to account for the confounding factor of phylogenetic relatedness in statistical analyses (Garamszegi, 2014). In PGLS, the phylogeny was used to account for phylogenetic pseudoreplication in the statistical models. We tested whether the latitudinal metrics of species (maximum, minimum, median and range, with actual or absolute values) could be explained by body size after controlling for sampling bias (by including the number of records as an additional predictor in the models) and for phylogenetic autocorrelation using PGLS. All predictors were scaled before running statistical models, in order to remove the effect of differences in scale and sampling units between variables (Zuur *et al.*, 2009). The PGLS and tests on phylogenetic signal were performed with the R package *caper* v.0.5.2 (Orme *et al.*, 2013).

We acknowledge that the phylogeny we used is not time calibrated and is only an approximation of the real phylogenetic relationships based on published reconstructions and taxonomic hierarchies, but no reliable DNA sequence data are currently available to obtain a phylogeny for the phylum. Nevertheless, even such a coarse phylogeny representing our current best knowledge could provide a more realistic error structure in the comparative models than no phylogeny at all (Garamszegi, 2014).

TESTING FOR THE HABITAT PRODUCTIVITY HYPOTHESIS

To address the possibility of habitat productivity being the driver of the body size–latitude relationship in marine tardigrades, we explicitly tested for this factor. We measured habitat productivity following Huston & Wolverton (2011), using marine ecologically and evolutionarily relevant net primary productivity (eNPP), which is the primary productivity during the growing season. These data were obtained from the carbon-based production model (CbPM) originally developed by Beherenfeld *et al.* (2005) and updated by Westberry *et al.* (2008). For each spatial grid with tardigrade occurrence in our dataset, we calculated the average net primary productivity of the most productive 3 months to obtain a metric of eNPP for each spatial grid.

We then included eNPP as an additional variable in our statistical models, testing its relevance in explaining differences in species richness and in body size (median, minimum and maximum), in comparison to the other variables included in the models.

BIPOLAR DISTRIBUTIONS

Many microorganisms have bipolar species distributions (Darling *et al.*, 2000), and this could lead

to interesting patterns of biogeographical structuring (see ‘Habitat selection hypothesis’ in the Discussion). Cold-tolerant species occur in cold climates of both hemispheres, but do not occur in the tropics. We looked for qualitative evidence of bipolar distributions in marine tardigrades by comparing the species composition in Northern and Southern Hemispheres for polar and temperate latitudes.

RESULTS

THE DATASET

Overall, 2340 records from 332 published papers for 209 taxa at species and subspecies level, found at latitudes from -66.0 to $+77.5^\circ$, were present in the dataset. Each taxonomic unit was cited by ≤ 163 papers, with a mean of 11.2 papers. Latitudinal ranges averaged 21.6° and spanned between single points for species known only for their type locality to almost 110° for common species with a latitudinally widespread distribution.

LATITUDINAL GRADIENTS IN SPECIES RICHNESS

The effect of the potential differences between the six main geographical areas in the world was enough to remove most of the confounding effect of spatial autocorrelation, and no spatial structure was observed; the non-spatial models were not significantly worse than the best spatial ones, apart from the spatial scale of 1° (Supporting Information, Table S1). The confounding factor of the number of records explained 65% of the variability in species richness, and the pattern was consistent at all spatial scales (Table 1; Supporting Information, Table S2). Thus, no apparent latitudinal gradient was found for species richness.

LATITUDINAL GRADIENTS IN BODY LENGTH

A hump-shaped increase in median body length with latitude was found (Table 2; Supporting Information, Table S3), consistently at all spatial scales (Supporting Information, Table S4), and the effect was significant for the Northern, but not for the Southern Hemisphere (Fig. 2; Supporting Information, Table S5).

The effect of latitude on minimum body length was also significant, with smaller species disappearing at higher latitudes (Table 2), especially in the Northern Hemisphere (Fig. 2). In contrast, almost no effect of latitude was found on maximum body length (Fig. 2; Table 2).

MECHANISTIC EXPLANATION

The explicit test on eNPP as a driver of changes in body size at the community level did not support the

Table 1. Results of the analyses of latitudinal gradients in species richness, accounting for the number of records, number of papers and subdivision into six main geographical areas, with square grids at 1°

Explanatory variable	<i>F</i>	<i>P</i>	lmg	RI
Six areas	1.73	–	0.007	0.27
Latitude (absolute)	1.42	0.2335	0.006	0.46
Latitude (squared)	2.51	0.1139	0.009	0.64
Papers	0.84	0.3608	0.227	0.37
Records	1318.44	< 0.0001	0.647	1.00
<i>R</i> ²	–	–	0.896	–

Results of linear models are reported because no spatial structure was detected at any scale (Supporting Information, Table S1). The table reports output as a type II test ANOVA table, with the *F*-value, *P*-value, partial *R*² (lmg) and relative importance (RI) for each explanatory variable. The sum of the total of the partial *R*² (lmg) represents the adjusted *R*² of each model. Significant *P*-values with an α -level = 0.001 are reported in bold.

hypothesis. The eNPP was not a significant predictor, and it had a marginal importance in all models we tested on species richness and on median, minimum and maximum body size (Table 3), where the confounding factor of sampling bias remained the only significant predictor.

PHYLOGENETIC EFFECTS

A phylogenetic signal, using the currently known, albeit not optimal, phylogenetic relationships between taxa (Supporting Information, Fig. S1), was present for body size (Pagel's $\lambda = 0.836$, $P < 0.0001$; Blomberg's $K = 0.766$, $P = 0.0010$), but not for latitudinal minimum, maximum and median values or latitudinal ranges, in either absolute or actual values (Supporting Information, Table S6). There was also no phylogenetic signal present in sampling bias, expressed as the number of records per species (Supporting Information, Table S6).

Body size was not artefactually affected by sampling bias; larger species were not those more easily recorded (PGLS: $t = 0.67$, $P = 0.501$). Differences in body size did not affect latitudinal metrics such as the minimum, maximum, median and range of latitude for each species, in either their absolute or actual values (Supporting Information, Table S7). In contrast, sampling bias, expressed as the number of records for each species, was positively correlated with latitudinal ranges, maximum and median values (Supporting Information, Table S7), i.e. more frequently recorded species had larger latitudinal ranges, regardless of potential phylogenetic constraints in body size and latitudinal ranges.

Table 2. Results of the analyses of latitudinal gradients in the median, minimum and maximum body size, accounting for absolute and quadratic forms of latitude, species richness and subdivision into six main geographical areas with square grids of 1°

Median	χ^2	<i>P</i>	lmg	RI
Six areas	2.99	0.7001	NA	0.02
Latitude (absolute)	6.56	0.0104	NA	0.99
Latitude (squared)	19.67	< 0.0001	NA	1.00
Richness	31.51	< 0.0001	NA	1.00
Minimum	<i>F</i>	<i>P</i>	lmg	RI
Six areas	0.63	0.6755	0.018	0.03
Latitude (absolute)	10.15	0.0015	0.060	1.00
Latitude (squared)	26.89	< 0.0001	0.101	1.00
Richness	110.55	< 0.0001	0.223	1.00
Maximum	χ^2	<i>P</i>	lmg	RI
Six areas	6.82	0.2347	NA	0.20
Latitude (absolute)	1.07	0.3009	NA	0.55
Latitude (squared)	5.74	0.0166	NA	0.99
Richness	85.02	< 0.0001	NA	1.00

Results of generalized least squares models with ratio spatial structure (for median and maximum) and linear models (for minimum) are reported depending on the best spatial structure found for each model (Supporting Information, Table S3). The table reports output as a type II test ANOVA table, with the *F*-value for linear models and χ^2 for generalized least squares, *P*-value, partial *R*² (lmg) for LMs, and relative importance (RI) for each explanatory variable. Significant *P*-values with an α -level = 0.001 are reported in bold. lmg calculated only for linear models; thus, “NA” is reported for generalized least squares.

HETEROTARDIGRADA VS. EUTARDIGRADA

One potential problem in the analyses is that most records (2306 out of 2340, 98.5%) are from 205 species and subspecies of class Heterotardigrada, whereas only a few (1.5%) are from four species in two genera of class Eutardigrada (*Halobiotus* Kristensen, 1982 and *Thulinus* Bertolani, 2003). Moreover, the few Eutardigrada are mostly distributed in the Northern Hemisphere (from 43.2 to 77.5°) and are large (from 407 to 666 µm); thus, they potentially bias any trend in body size and phylogenetic effects. We repeated the analyses on Heterotardigrada only and, in comparison to the analyses on all marine Tardigrada: (1) no changes were found regarding latitudinal gradients in species richness (Supporting Information, Tables S8 and S9); (2) the latitudinal gradient in median body size disappeared (Supporting Information, Tables S10 and S11); the latitudinal gradient in minimum body size held true (Supporting Information, Tables S12 and S13), and the lack of such a gradient for maximum body size was confirmed (Supporting Information, Tables S14 and S15).

BIPOLAR DISTRIBUTIONS

We looked for bipolar distributions in marine tardigrades by comparing species composition in Northern and

Southern Hemispheres for polar and temperate latitudes (Table 4). Far southern latitudes are poorly studied, but based on the existing records there appears to be very little overlap between species in the two hemispheres. No overlapping species have been reported from 40–70° latitude. Only seven out of 106 species (6.6%) reported from 30–40° latitude have been found in both hemispheres, and out of a total of 154 species reported from 30–70° latitude only 4.5% have been found in both.

DISCUSSION

LATITUDINAL GRADIENTS IN SPECIES DIVERSITY

We found no evidence of a latitudinal gradient in species diversity in marine tardigrades. Instead, variation in diversity was largely determined by sampling effort as measured by the number of records. In other words, a map of tardigrade diversity is simply a map of tardigradologists. This was previously noted for marine tardigrades by Kristensen & Mackness (2000). Likewise, rotifer distributions are determined largely by the number of rotiferologists (Dumont, 1983; Fontaneto *et al.*, 2012). Undersampling is a persistent problem for biogeographical studies (Foissner, 2006; Smith *et al.*, 2006; Finlay & Estaban,

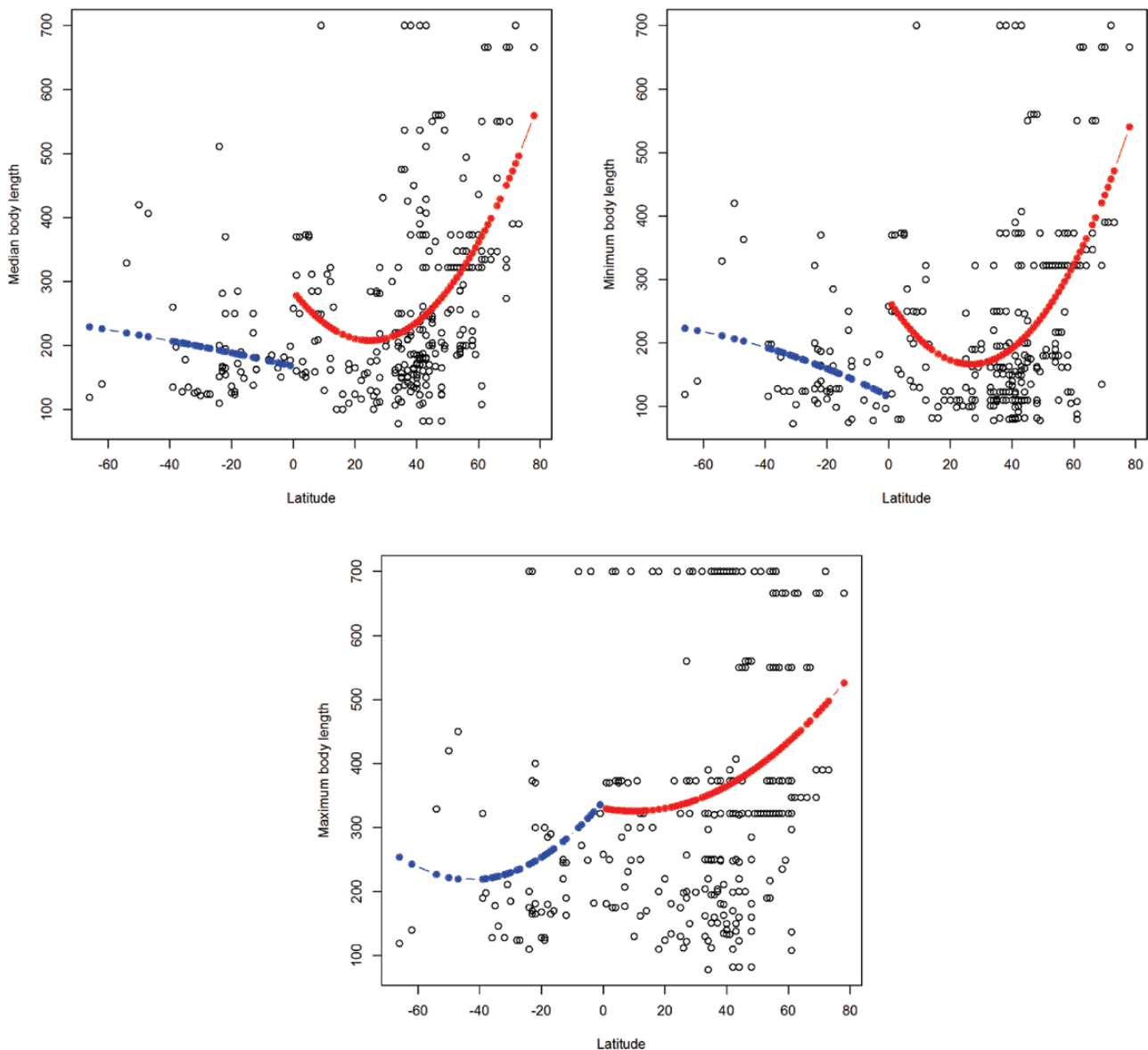


Figure 2. Relationship between median, minimum and maximum body length (as proxies for community-level body size) and latitude for squared grids of 1° latitude and longitude. Relationships are depicted separately for the Northern (red dots and lines) and the Southern (blue dots and lines) Hemisphere.

2007; Azovsky & Mazei, 2013), and this is clearly true in marine tardigrades, for which many understudied and unstudied areas remain (Fig. 1). Moreover, a large bias in the dataset is related to habitat; most records (91.5%) are for strictly tidal species. We consider these results rather strong, given that potential confounding factors in the data, such as differences in grid area or other types of geographical bias, would have a similar effect on all the variables analysed.

Other large-scale studies of marine invertebrate diversity and latitude have shown mixed results. The coastal European marine macrozoobenthos was studied

by Hummel *et al.* (2016) for the latitudinal range from 30 to 60°N, and they observed the highest diversity at latitudes between 40 and 45°N, whereas clearly lower diversity was found at lower and higher latitudes. They concluded that local environmental factors overcame latitudinal effects. Hillebrand & Azovsky (2001) observed no correlation between latitude and the species richness of diatoms in the Northern Hemisphere, whereas a negative correlation was found in the Southern Hemisphere. However, Hillebrand & Azovsky (2001) concluded that the latitudinal decrease of species richness in the Southern Hemisphere was

Table 3. Results of the analyses of latitudinal gradients in species richness and body size (median, minimum and maximum) while searching for the mechanistic explanation of habitat productivity (eNPP)

Richness	<i>F</i>	<i>P</i>	lmg	RI
Six areas	1.92	0.0899	0.007	0.34
Latitude (absolute)	2.89	0.0898	0.005	0.45
Latitude (squared)	4.08	0.0441	0.007	0.72
Papers	0.15	0.6978	0.222	0.28
Records	1223.67	< 0.0001	0.649	1.00
eNPP	4.32	0.0385	0.004	0.63
<i>R</i> ²	—	—	0.894	—
Median	χ^2	<i>P</i>	lmg	RI
Six areas	8.99	0.1091	NA	0.01
Latitude (absolute)	5.62	0.0178	NA	0.72
Latitude (squared)	12.32	0.0004	NA	0.97
Papers	0.28	0.5931	NA	0.04
Records	9.60	0.0019	NA	0.95
eNPP	2.19	0.1392	NA	0.05
Minimum	χ^2	<i>P</i>	lmg	RI
Six areas	7.94	0.1593	NA	0.01
Latitude (absolute)	7.14	0.0076	NA	0.70
Latitude (squared)	13.91	0.0002	NA	0.96
Papers	0.81	0.3688	NA	0.05
Records	57.11	< 0.0001	NA	1.00
eNPP	1.91	0.1672	NA	0.06
Maximum	χ^2	<i>P</i>	lmg	RI
Six areas	11.90	0.0362	NA	—
Latitude (absolute)	0.91	0.3409	NA	—
Latitude (squared)	3.23	0.0720	NA	—
Papers	0.89	0.3463	NA	—
Records	40.66	< 0.0001	NA	—
eNPP	3.95	0.0467	NA	—

The models include the same variables as in Tables 1 and 2, in addition to eNPP. Results of linear models are reported for richness, and generalized least squares with an exponential spatial structure for median and minimum body length. The table reports output as a type II test ANOVA table, with the *F*-value for linear models and χ^2 for generalized least squares, *P*-value, partial *R*² (lmg) and relative importance (RI) for each explanatory variable. The sum of the total of the partial *R*² (lmg) represents the adjusted *R*² of each model. Significant *P*-values with an α -level = 0.001 are reported in bold. lmg calculated only for linear models; thus, “NA” is reported for generalized least squares.

an artefact caused by poor sampling data, which in the Southern Hemisphere relied on only three studies from Antarctic lakes (two of which were represented by only one sample each). In a meta-analysis of European deep and shallow seas, Narayanaswamy *et al.* (2013) found statistically significant increases in diversity with increasing latitude for both macrofauna and meiofauna.

LATITUDINAL GRADIENTS IN BODY SIZE

Even with our relatively small database, substantial geographical sampling bias, and other confounding factors not included in the analyses, our results showed a significant positive relationship between latitude and body size. Marine tardigrades seem to have latitudinal gradients in body size. Specific findings were as follows:

Table 4. Number of species and number of research papers in polar and temperate regions comparing Northern and Southern Hemispheres

Latitude (absolute value)	Northern Hemisphere		Southern Hemisphere		Shared species
	Species	Papers	Species	Papers	
50–70	41	84	3	3	0
40–50	110	153	2	1	0
30–40	94	70	19	7	7
30–70	137	272	24	11	7

Shared species are those found in both hemispheres. The total number of species (from 30 to 70° latitude) are not simple sums of the three sub-bands, owing to species overlap.

1. There was a significant increase in median and minimum body size with latitude for the Northern Hemisphere but not for the Southern Hemisphere.
2. Latitude had almost no effect on maximum body size.
3. In the Northern Hemisphere, species with the smallest body sizes disappeared at high latitudes, whereas the largest sized species were found across all latitudes.
4. The body size–latitude curve in the Northern Hemisphere was hump shaped (highest body size at high latitudes, lowest ~25°, then a slight increase in the tropics).
5. Removal of the larger and more northerly eutardigrades from the analysis had no effect on the results for species richness or for minimum or maximum body size.
6. The assessment of potential phylogenetic effects, albeit based on a potentially weak phylogeny, showed that related species were similar in body size but not in latitudinal distribution; therefore, phylogeny did not impact the body size–latitude relationship.
7. Bipolar species distributions did not occur.

To our knowledge, this is the first evidence of potential latitudinal gradients in body size in any microscopic organism. The single previous study was for monogenean parasites (Poulin, 1996), although these are not exclusively microscopic in size. The majority of species are < 1 mm in body length, but the analysis was done on family and generic levels, and the vast majority of families and genera are macroscopic. In any case, at the family level a positive relationship was found between body size and latitude, but the correlation was not statistically significant. At the generic level, only two of 39 families showed significant relationships between body size and latitude, and these were not the microscopic genera.

DRIVERS OF LATITUDINAL GRADIENTS IN BODY SIZE FOR MARINE TARDIGRADES

The initial mechanism proposed for latitudinal gradients in body size in homeotherms was heat conservation, owing to the lower surface area-to-volume ratio in larger individuals (Bergmann, 1847; Watt *et al.*, 2010; Sommer *et al.*, 2017). This has been named Bergmann's rule, but it is an unlikely driver in most poikilotherms (Blackburn *et al.*, 1999; Blanckenhorn & Demont, 2004), and it is certainly not a factor in microorganisms because they instantaneously match ambient temperatures (Stevenson, 1985). The body size–latitude response is more variable in poikilotherms than in homeotherms, suggesting that a single underlying process is unlikely in poikilotherms (Berke *et al.*, 2013), although others are still hopeful of a unifying explanation (Daufresne *et al.*, 2009; Watt *et al.*, 2010; Huston & Wolverson, 2011; Classen *et al.*, 2017).

The pattern we observed in the Northern Hemisphere was a reduction in the proportion of smaller species at higher latitude. This is what Daufresne *et al.* (2009) termed a 'species shift'. James's rule (James, 1970), the intraspecific change in body size between populations (a 'population body size shift'), was not involved, because our measure of body size was the maximum reported in the literature for each species regardless of its location. Much of the speculation about mechanisms for body size–latitude gradients has been based on intraspecific responses (Ray, 1960; Atkinson, 1994; Blackburn *et al.*, 1999; Atkinson *et al.*, 2003; Angilletta & Dunham, 2003; Angilletta *et al.*, 2004a, b; Forster *et al.*, 2012; Berke *et al.*, 2013), but some could scale up to community-based changes through extinction and speciation operating differently on small- and large-bodied species. The following hypotheses are not necessarily exclusive.

Habitat selection hypothesis ('everything is everywhere, but the environment selects')

Biogeographical patterns can be expected in microorganisms even if they have huge populations,

unlimited dispersal capabilities and near-cosmopolitan distributions (Fenchel & Finlay, 2004; Fontaneto & Hortal, 2013; Heger *et al.*, 2013). This can occur through niche specialization and was described by Baas-Becking's original phrase 'everything is everywhere, and the environment selects' (Baas-Becking, 1934; De Wit & Bouvier, 2006). This usually creates local habitat differences in community structure, but it could also create global patterns. For example, freshwater protists may be found in streams or ponds over the entire world (Finlay & Esteban, 2007), but they are found only in freshwater. Marine tardigrade species are found only in oceans and seas. More interesting latitudinal species distribution patterns can also be produced by habitat selection. Bipolar distributions are known in many cold-loving microbes, and genetic connectivity has been demonstrated in some cases (Darling *et al.*, 2000). Water temperature could be such a selection factor for marine tardigrades (Faurby & Funch, 2011; Faurby *et al.*, 2012; Faurby & Barber, 2015), and it is possible that this would result in latitudinal differences in marine tardigrade species distributions. The comparison between overlap in species occurrence between Northern and Southern Hemispheres apparently does not support a role of water temperature regardless of geographical distances; no overlapping species have been reported at higher (and colder) north and south latitudes, whereas the degree of overlap increases towards lower latitudes, where the effect of similarity in temperatures is confounded by geographical proximity.

A recent survey of the Bahamas reported 17 marine tardigrade species (Bartels *et al.*, 2018). Twenty-nine species have been reported from the Caribbean Sea and 42 from Atlantic North America. These numbers appear much lower than the 74 recorded from the intensively studied Mediterranean (Bartels *et al.*, 2016). These constitute respectively 8, 14, 20 and 35% of the global total marine tardigrade diversity. In contrast, Fenchel & Finlay (2004) found 50% of all named flagellates in one bay in Denmark. Regional marine tardigrade diversity is lower compared with global diversity than in many microorganisms. Furthermore, we found no bipolar distributions in marine tardigrades, and there is little overlap between species in the temperate Northern and Southern Hemispheres. This hypothesis is not supported for marine tardigrades.

Differential dispersal hypothesis

Contrary to the habitat selection hypothesis, it is likely that marine tardigrades do not have unlimited dispersal ability. Adult dispersal does occur (Fontaneto, 2019). Suspended active adults have been found in the water column and, in a small number of species, buoyancy mechanisms are known that might facilitate

passive dispersal (Jørgensen & Kristensen, 2001). However, marine tardigrades are benthic, cannot swim and do not have a planktonic larval stage. Most marine tardigrades probably lack the cryptobiotic ability of limnoterrestrial tardigrades and do not form the 'tuns' that are likely to be dispersal propagules in terrestrial tardigrades (Kinchin, 1994). Only two exceptions to this are currently known, and these are supralittoral or littoral species (Jørgensen & Møbjerg, 2014; Hygum *et al.*, 2016). Additionally, although marine tardigrades are sometimes found in high densities [e.g. 3500 specimens of *Batillipes pennaki* Marcus, 1946 per 100 cm³ of beach sand (Giere, 2013)], they are usually much less numerous than nematodes and copepods, and the number of specimens per sample is usually low (Kinchin, 1994; Gallo D'Addabbo *et al.*, 1999; Giere, 2013; Fontoura *et al.*, 2017).

Size-related differences in dispersal ability could create latitudinal clines (Blackburn & Gaston, 1996; Blackburn *et al.*, 1999; Vinarski, 2014), if larger species disperse further and if lower latitudes are the predominant source for dispersal to higher latitudes. We have no evidence of dispersal ability and size in tardigrades, but excluding special buoyancy mechanisms, larger species should sink faster than small species based on Stoke's law (Reynolds, 1984, 1994). Additionally, Jenkins *et al.* (2007) and Rundle *et al.* (2007) found that larger size did not increase dispersal distance in passive dispersers. It is also possible that body size has little to do with settlement in small organisms, because most settlement occurs in aggregated masses of marine snow (Sommer *et al.*, 2017). In marine tardigrades, if body size has any impact at all on dispersal ability, dispersal should be higher in small species. This hypothesis is unlikely to be substantiated in marine tardigrades.

Predation hypothesis

The predation hypothesis and the resource availability hypothesis (see next subsection) suggest that differential survival rather than differential dispersal drives differences in body size at various latitudes, but unlike the habitat selection hypothesis, all species are not dispersed globally, and bipolar or cosmopolitan distributions are not expected to be common. The predation hypothesis requires that predation pressure differs with latitude and that body size increases with predation pressure. Given that species diversity is generally higher at lower latitudes, predation and other factors should be stronger there. This was documented by predator exclusion experiments for macroscopic benthic marine invertebrates (Freestone *et al.*, 2011). Higher predation in warmer, drier climates led to an increase in body size in spiders (Entling *et al.*, 2010), whereas in phytoplankton, grazing by planktivores led

to a species shift reducing mean phytoplankton cell size rather than increasing it (Sommer *et al.*, 2017). Based on life-history theory, Angilletta *et al.* (2004a, b) and Atkinson (1994) discussed the possibility that high juvenile mortality from predation could select for shorter development times and reduced maximum body size within species and that this could favour smaller individuals in warmer climates. If this were translated to community-level changes, this could increase the proportion of small species at low latitudes, but it would not explain the occurrence of many large species there. Several authors have concluded that predation is an unlikely mechanism in general for body size–latitudinal gradients in poikilotherms (Lindsey, 1966; Atkinson, 1994; Vinarski, 2014), and it seems an unlikely mechanism for the pattern we observed in marine tardigrades.

Resource availability hypothesis

Resource quality might be higher at higher latitudes, and this could allow individuals and species to attain larger body sizes (Geist, 1987; Ho *et al.*, 2009; McNab, 2010; Huston & Wolverton, 2011) or seasonal fluctuations in resource availability could favour large body size owing to starvation resistance (Lindstedt & Boyce, 1985; Cushman *et al.*, 1993; Blackburn *et al.*, 1999). It has also been argued that reduced biotic pressure at high latitudes could allow larger body size through increased access to resources (Zaveloff & Boyce, 1988; Moran & Woods, 2012).

Latitudinal patterns in resource availability in marine systems were not correlated with the body size of marine tardigrades. Huston & Wolverton (2011) demonstrated that eNPP is the single most important predictor of community-level body size for marine fish. Unfortunately, including eNPP in our models did not change the effects of the main results; eNPP was never a significant predictor, and it explained only a negligible proportion of the variance in all models. This is a surprising result given that a rough visual interpretation of the trends in Figure 2 would suggest a close relationship with ocean eNPP (Behrenfeld *et al.*, 2005), including a peak in body size at the peak in eNPP at the equatorial upwelling, lower eNPP in the southern oceans, and a dramatic increase in eNPP and tardigrade body size in the northern oceans. The lack of a relationship between community-level tardigrade body size and eNPP could be a result of problems in our dataset. For example, marine tardigrade records were from vastly different depths. However, the vast majority of records were from shallow waters (not allowing us also to test for potential differences between habitats); therefore, we doubt that this had a large impact. Another problem could be the small sample size of our dataset, but even

with this small sample size we were able to identify the latitudinal body size pattern. Overall, the question about which process could drive the observed patterns remains open.

In addition to eNPP, oxygen availability might be a limiting factor for aquatic poikilotherms (Atkinson, 1994; Chapelle & Peck, 1999; Makarieva *et al.*, 2005). Gas exchange is directly related to surface area-to-volume ratios, and this would favour smaller body sizes in warmer temperatures where the dissolved oxygen is lower. Huston & Wolverton (2011) believe this could work in conjunction with eNPP to control body size in aquatic systems. However, this does not explain the reduced number of small species at high latitudes or the common occurrence of large species in the tropics that we observed.

Additional support for the resource availability hypothesis can be found in the studies by Lindsey (1966), Zaveloff & Boyce (1988), Cushman *et al.* (1993), Atkinson *et al.* (2003), Jones *et al.* (2005), Ho *et al.* (2009) and Sommer *et al.* (2017).

The temperature–size rule and the metabolic theory of ecology

At the intraspecific level, a decrease in final cell or body size with an increase in rearing temperature might be a nearly universal response (Ray, 1960; Lindsey, 1966; Atkinson, 1994; Van Voorhies, 1996; Gardner *et al.*, 2011). This relationship occurs because higher developmental rates force trade-offs that lead to lower final body size (Ohlberger, 2013). This has been called the temperature–size rule (Atkinson, 1994; Daufresne *et al.*, 2009; Sommer *et al.*, 2017). The temperature–size rule is governed by basic metabolic impacts of the surface area-to-volume relationship and associated life-history ramifications (Atkinson, 1994; Angilletta *et al.*, 2004a, b). Daufresne *et al.* (2009) suggested that the temperature–size rule might relate to the metabolic theory of ecology (Brown *et al.*, 2004), and the metabolic theory of ecology predicts that at warmer temperatures there should be a decrease in body size and/or a decrease in population size. A reduction in population size of large species could make them more prone to extinction, thus forming a potential bridge between intraspecific and interspecific body size–temperature patterns. A linkage between intraspecific temperature–size effects and community-level species shifts has been documented in phytoplankton studies, but the nature of this linkage and whether it is mediated directly by temperature is still controversial (Sommer *et al.*, 2017). Examining the links between population shifts in body size and species shifts in body size would be difficult in marine tardigrades but necessary to evaluate this hypothesis.

POLAR GIGANTISM

Unusually large polar species are known from numerous taxa (pycnogonids, copepods, pteropods, chaetognaths, sponges, etc.) and could represent the high-latitude endpoint of a latitudinal size gradient (Moran & Woods, 2012). We did not find a significant increase in maximum body size (largest species) with latitude; therefore, this is not responsible for body size–latitudinal gradients in marine tardigrades, but we examined our database to find out whether there are polar ‘tardigrades of unusual size’ (TOUSes, with our apologies to ‘The Princess Bride’). A common definition of gigantism is species in the 95th percentile of body size within a clade (Chapelle & Peck, 1999; Moran & Woods, 2012). The body size distribution for marine tardigrades is shown in Figure 3, in which any species > 400 µm body length would be in the 95th percentile. There are only nine species of this size, and three of these are greater than three times the mean body size. *Coronarctus laubieri* Renaud-Mornant, 1987, *Echiniscoides sigismundi porphyrae* Grimaldi de Zio, Gallo D’Addabbo & Pietanza, 2000, *Ecn. travei* Bellido & Bertrand, 1981, *Florarctus heimi* Delamare Deboutteville & Renaud-Mornant, 1965, *Hab. stenostomus* (Richters, 1908) and *Thu. itoi* (Tsurusaki, 1980) are between 400 and 600 µm long,

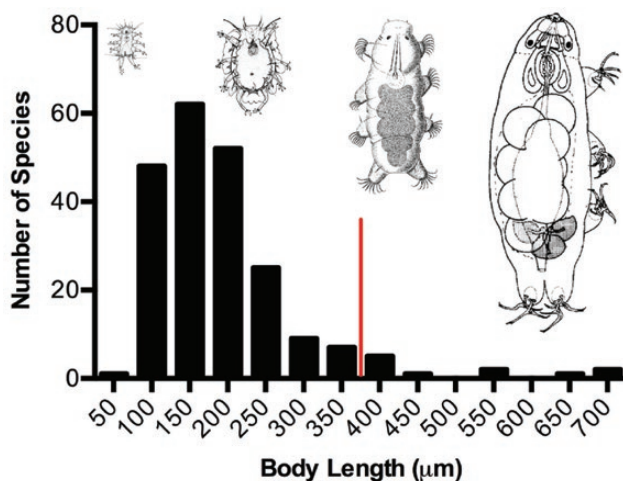


Figure 3. Frequency distribution of maximum body length reported for marine tardigrade species. Red line indicates 95th percentile. Drawings are approximately to scale and represent, from left to right, the smallest marine tardigrade (*Dipodactylus australiensis* Jorgensen, Boesgaard, Mobjerg, & Kristensen, 2014, 73 µm), a species with average body size (*Florarctus acer*, 195 µm), a species slightly above the 95th percentile (*Ecn. sigismundi porphyrae*, 450 µm) and the largest marine tardigrade (*Hab. arcturilius*, 700 µm). Tardigrade images are redrawn from Jørgensen *et al.* (2014), Renaud-Mornant (1989), Schultze (1865) and Crisp & Kristensen (1983).

and *Bat. pennaki*, *Hab. arcturilius* Crisp & Kristensen, 1983 and *Hab. crispae* Kristensen, 1982 are between 600 and 700 µm long. Four of these are eutardigrades (*Thu. itoi* and the three *Halobiotus* species), which are generally larger than heterotardigrades, as previously mentioned, and they are not particularly large compared with their terrestrial relatives. *Hab. arcturilius* is one of the largest marine tardigrades, and it is exclusively arctic. None of the large heterotardigrades is polar, and *Bat. pennaki* (equal in size to *Hab. arcturilius*) is broadly distributed from the tropics to cold temperate regions. In addition, a phylogenetic signal was found for body size, but not for latitudinal ranges. Arctic TOUSes exist, but polar gigantism does not.

NORTHERN VS. SOUTHERN HEMISPHERE

The body size–latitude relationship in marine tardigrades was statistically significant for the Northern Hemisphere but not for the Southern Hemisphere, and the shape of the curves differed greatly (Fig. 2). This could be attributable to undersampling in the south, especially at higher latitudes. However, different latitudinal effects between hemispheres have been found in numerous studies of other marine organisms (Hildebrand & Azovsky, 2001; Blanchet *et al.*, 2010; Peck & Harper, 2010; Huston & Wolverson, 2011; Moran & Woods, 2012; Berke *et al.*, 2013; Azovsky & Mazei, 2013). High latitudes in the Southern Hemisphere are dominated by the circumglobal Southern Ocean, and they have much less land mass than in the Northern Hemisphere. Therefore, there is less coastal habitat, which is the main habitat for marine tardigrades. Together with a distinct geological history of the Antarctic compared with the Arctic, unique biogeographical patterns would not be unexpected in the two hemispheres (Moran & Woods, 2012; Clarke & Johnston, 2003; Chown & Convey, 2007; Waters, 2008; Czechowski *et al.*, 2012). It will be interesting to see whether the hemispherical differences we observed in marine tardigrades change as new records accumulate from the Southern Ocean.

ACKNOWLEDGEMENTS

We thank Warren Wilson College and East Tennessee State University for ongoing support. Dr Michael Huston was helpful with our analysis of eNPP. We thank the editors of the special issue, Søren Faurby and other anonymous reviewers for their helpful comments that improved the strength of the study. This study was supported, in part, by a SYNTHESYS grant (no. FR-TAF-6211 to Ł.K.). Studies have been

conducted, in part, in the framework of activities of the BARg (Biodiversity and Astrobiology Research group).

REFERENCES

- Altiero T, Sukuzi A, Rebecchi L. 2018.** Chapter 8. Reproduction, development and life cycles. In: Schill RO, ed. *Water bears: the biology of tardigrades*. *Zoological Monographs* **2**: 211–247.
- Angilletta MJ Jr, Dunham AE. 2003.** The temperature-size rule in ectotherms: simple evolutionary explanations may not be general. *The American Naturalist* **162**: 332–342.
- Angilletta MJ Jr, Niewiarowski PH, Dunham AE, Leaché AD, Porter WP. 2004a.** Bergmann's clines in ectotherms: illustrating a life-history perspective with sceloporine lizards. *The American Naturalist* **164**: E168–E183.
- Angilletta MJ Jr, Steury TD, Sears MW. 2004b.** Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integrative and Comparative Biology* **44**: 498–509.
- Atkinson D. 1994.** Temperature and organism size: a biological law for ectotherms? *Advances in Ecological Research* **25**: 1–58.
- Atkinson D, Ciotti BJ, Montagnes DJS. 2003.** Protists decrease in size linearly with temperature: ca. 2.5% °C⁻¹. *Proceedings of the Royal Society B: Biological Sciences* **270**: 2605–2611.
- Azovsky A, Mazei Y. 2013.** Large-scale patterns in the diversity and distribution of marine benthic ciliates: do microbes have macroecology? *Global Ecology and Biogeography* **22**: 163–172.
- Baas-Becking LGM. 1934.** *Geobiologie of Inleiding tot de Milieukunde*. The Hague: W. P. Van Stockum & Zoon.
- Bartels PJ, Apodaca JJ, Mora C, Nelson DR. 2016.** A global biodiversity estimate of a poorly known taxon: phylum Tardigrada. *Zoological Journal of the Linnean Society* **178**: 730–736.
- Bartels PJ, Fontoura P, Nelson DR. 2018.** Marine tardigrades of the Bahamas with the description of two new species and updated keys to the species of *Anisonyches* and *Archechiniscus*. *Zootaxa* **4420**: 43–70.
- Bartels PJ, Kaczmarek Ł, Roszkowska M, Nelson DR. 2015.** Interactive map of marine tardigrades of the world. Available at: <https://fusiontables.google.com/DataSource?docid=1nw0Nct7GW7M-geDHq91fycBMljUymCzNEaUqjF6q&pli=1-map:id=3> (last accessed 20 October 18).
- Behrenfeld MJ, Boss E, Siegel DA, Shea DM. 2005.** Carbon-based ocean productivity and phytoplankton physiology from space. *Global Biogeochemical Cycles* **19**: 1–14.
- Bergmann C. 1847.** Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Gottinger Studien* **1**: 595–708.
- Berke SK, Jablonski D, Roy K, Tomasovych A. 2013.** Beyond Bergmann's rule: size–latitude relationships in marine Bivalvia world-wide: size–latitude trends in bivalves. *Global Ecology and Biogeography* **22**: 173–183.
- Blackburn TM, Gaston KJ. 1996.** Spatial patterns in the body sizes of bird species in the New World. *Oikos* **77**: 436–446.
- Blackburn TM, Gaston KJ, Loder N. 1999.** Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distributions* **5**: 165–174.
- Blanchet S, Grenouillet G, Beauchard O, Tedesco PA, Leprieur F, Dürr HH, Busson F, Oberdorff T, Brosse S. 2010.** Non-native species disrupt the worldwide patterns of freshwater fish body size: implications for Bergmann's rule. *Ecology Letters* **13**: 421–431.
- Blanckenhorn WU, Demont M. 2004.** Bergmann and converse Bergmann latitudinal clines in arthropods: two ends of a continuum? *Integrative and Comparative Biology* **44**: 413–424.
- Blomberg SP, Garland T Jr, Ives AR. 2003.** Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**: 717–745.
- Brown JH, Allen AP, Gillooly JF. 2007.** The metabolic theory of ecology and the role of body size in marine and freshwater ecosystems. In: Hildrew AG, Raffaelli DG, Edmonds-Brown R, eds. *Body size: the structure and function of aquatic ecosystems*. Cambridge: Cambridge University Press, 1–15.
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004.** Toward a metabolic theory of ecology. *Ecology* **85**: 1771–1789.
- Burnham KP, Anderson DR. 2002.** *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer Science+Business Media, Inc.
- Chapelle G, Peck LS. 1999.** Polar gigantism dictated by oxygen availability. *Nature* **399**: 114–115.
- Chevan A, Sutherland M. 1991.** Hierarchical partitioning. *American Statistician* **45**: 90–96.
- Chown SL, Convey P. 2007.** Spatial and temporal variability across life's hierarchies in the terrestrial Antarctic. *Philosophical Transactions of the Royal Society B: Biological Sciences* **362**: 2307–2331.
- Clarke A, Johnston NM. 2003.** Antarctic marine benthic diversity. *Oceanography and Marine Biology* **41**: 47–114.
- Classen A, Steffan-Dewenter I, Kindeketa WJ, Peters MK. 2017.** Integrating intraspecific variation in community ecology unifies theories on body size shifts along climatic gradients. *Functional Ecology* **31**: 768–777.
- Clausen LKB, Andersen KN, Hygum TL, Jørgensen A, Møbjerg N. 2014.** First record of cysts in the tidal tardigrade *Echiniscoides sigismundi*. *Helgoland Marine Research* **68**: 531–537.
- Crawley MJ. 2012.** *The R book, 2nd edn*. Chichester: Wiley.
- Crisp M, Kristensen, RM. 1983.** A new marine interstitial eutardigrade from East Greenland, with comments on habitat and biology. *Videnskabelige Meddelelser Dansk Naturhistorisk Forening* **144**: 99–114.
- Cushman JH, Lawton JH, Manly BF. 1993.** Latitudinal patterns in European ant assemblages: variation in species richness and body size. *Oecologia* **95**: 30–37.
- Czechowski P, Sands CJ, Adams BJ, D'Haese CA, Gibson JAE, McInnes SJ, Stevens MI. 2012.** Antarctic Tardigrada: a first step in understanding molecular operational taxonomic units (MOTUs) and biogeography of cryptic meiofauna. *Invertebrate Systematics* **26**: 526–538.

- Darling KF, Wade CM, Stewart IA, Kroon D, Dingle R, Brown AJ. 2000.** Molecular evidence for genetic mixing of Arctic and Antarctic subpolar populations of planktonic foraminifers. *Nature* **405**: 43–47.
- Daufresne M, Lengfellner K, Sommer U. 2009.** Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* **106**: 12788–12793.
- Degma P, Bertolani R, Guidetti R. 2009–2018.** *Actual checklist of Tardigrada species (version 33: 15-10-2017)*.
- Degma P, Guidetti R. 2007.** Notes to the current checklist of Tardigrada. *Zootaxa* **1579**: 41–53.
- Dumont HJ. 1983.** Biogeography of rotifers. *Hydrobiologia* **104**: 19–30.
- Entling W, Schmidt-Entling MH, Bacher S, Brandl R, Nentwig W. 2010.** Body size–climate relationships of European spiders. *Journal of Biogeography* **37**: 477–485.
- Faurby S, Barber PH. 2015.** Extreme population subdivision despite high colonization ability: contrasting regional patterns in intertidal tardigrades from the west coast of North America. *Journal of Biogeography* **42**: 1006–1017.
- Faurby S, Funch P. 2011.** Size is not everything: a meta-analysis of geographic variation in microscopic eukaryotes: geographic variation in microscopic organisms. *Global Ecology and Biogeography* **20**: 475–485.
- Faurby S, Jørgensen A, Kristensen RM, Funch P. 2012.** Distribution and speciation in marine intertidal tardigrades: testing the roles of climatic and geographical isolation: distribution and speciation in tidal tardigrades. *Journal of Biogeography* **39**: 1596–1607.
- Fenchel T, Finlay BJ. 2003.** Is microbial diversity fundamentally different from biodiversity of larger animals and plants? *European Journal of Protistology* **39**: 486–490.
- Fenchel T, Finlay BJ. 2004.** The ubiquity of small species: patterns of local and global diversity. *AIBS Bulletin* **54**: 777–784.
- Finlay BJ, Esteban GF. 2007.** Body size and biogeography. In: Hildrew AG, Raffaelli DG, Edmonds-Brown R, eds. *Body size: the structure and function of aquatic ecosystems*. Cambridge: Cambridge University Press, 167–185.
- Foissner W. 1999.** Protist diversity: estimates of the near-imponderable. *Protist* **150**: 363–368.
- Foissner W. 2006.** Biogeography and dispersal of micro-organisms: a review emphasizing protists. *Acta Protozoologica* **45**: 111–136.
- Fontaneto D. 2011.** *Biogeography of microscopic organisms: is everything small everywhere?* New York: Cambridge University Press.
- Fontaneto D. 2019.** Long-distance passive dispersal in microscopic aquatic animals. *Movement Ecology* **7**: 10.
- Fontaneto D, Barbosa AM, Segers H, Pautasso M. 2012.** The ‘rotiferologist’ effect and other global correlates of species richness in monogonont rotifers. *Ecography* **35**: 174–182.
- Fontaneto D, Hortal J. 2013.** At least some protist species are not ubiquitous. *Molecular Ecology* **22**: 5053–5055.
- Fontoura P, Bartels PJ, Jørgensen A, Kristensen RM, Hansen JG. 2017.** A dichotomous key to the genera of the marine heterotardigrades (Tardigrada). *Zootaxa* **4294**: 1–45.
- Forster J, Hirst AG, Atkinson D. 2012.** Warming-induced reductions in body size are greater in aquatic than terrestrial species. *Proceedings of the National Academy of Sciences of the United States of America* **109**: 19310–19314.
- Fox J, Weisberg S. 2011.** *An {R} companion to applied regression, 2nd edn*. Thousand Oaks: Sage.
- Freestone AL, Osman RW, Ruiz GM, Torchin ME. 2011.** Stronger predation in the tropics shapes species richness patterns in marine communities. *Ecology* **92**: 983–993.
- Fujimoto S, Jørgensen A, Hansen JG. 2016.** A molecular approach to arthrotardigrade phylogeny (Heterotardigrada, Tardigrada). *Zoologica Scripta* **46**: 496–505.
- Gallo D’Addabbo M, de Zio Grimaldi S, Morone MRL, Pietanza R, D’Addabbo R, Todaro MA. 1999.** Diversity and dynamics of an interstitial Tardigrada population in the Meloria Shoals, Ligurian Sea, with a redescription of *Batillipes similis* (Heterotardigrada, Batillipidae). *Italian Journal of Zoology* **66**: 51–61.
- Garamszegi LZ. 2014.** *Modern phylogenetic comparative methods and their application in evolutionary biology*. Berlin: Springer.
- Gardner JL, Peters A, Kearney MR, Joseph L, Heinsohn R. 2011.** Declining body size: a third universal response to warming? *Trends in Ecology & Evolution* **26**: 285–291.
- Garraffoni AR, Balsamo M. 2017.** Is the ubiquitous distribution real for marine gastrotrichs? Detection of areas of endemism using parsimony analysis of endemism (PAE). *Proceedings of the Biological Society of Washington* **130**: 197–210.
- Geist V. 1987.** Bergmann’s rule is invalid. *Canadian Journal of Zoology* **65**: 1035–1038.
- Giere O. 2013.** *Meiobenthology: the microscopic fauna in aquatic sediments*. Berlin: Springer-Verlag.
- Giere O. 2019.** *Perspectives in meiobenthology: reviews, reflections and conclusions*. Cham: Springer-Nature.
- Guidetti R, Bertolani R. 2005.** Tardigrade taxonomy: an updated check list of the taxa and a list of characters for their identification. *Zootaxa* **845**: 1–46.
- Heger TJ, Mitchell EA, Leander BS. 2013.** Holarctic phylogeography of the testate amoeba *Hyalosphenia papilio* (Amoebozoa: Arcellinida) reveals extensive genetic diversity explained more by environment than dispersal limitation. *Molecular Ecology* **22**: 5172–5184.
- Hildrew AG, Raffaelli DG, Edmonds-Brown R. 2007.** *Body size: the structure and function of aquatic ecosystems*. Cambridge: Cambridge University Press.
- Hillebrand H. 2004.** On the generality of the latitudinal diversity gradient. *The American Naturalist* **163**: 192–211.
- Hillebrand H, Azovsky AI. 2001.** Body size determines the strength of the latitudinal diversity gradient. *Ecography* **24**: 251–256.
- Ho C-K, Pennings SC, Carefoot TH. 2009.** Is diet quality an overlooked mechanism for Bergmann’s rule? *The American Naturalist* **175**: 269–276.
- Hummel H, Van Avesaath P, Wijnhoven S, Kleine-Schaars L, Degraer S, Kerckhof F, Bojanic N, Skejic S, Vidjak O, Rousou M, Orav-Kotta H, Kotta J, Jourde J,**

- Pedrotti ML, Leclerc J-C, Simon N, Rigaut-Jalabert F, Bachelet G, Lavesque N, Arvanitidis C, Pavludi C, Faulwetter S, Crowe T, Coughlan J, Benedetti-Cecchi L, Dal Bello M, Magni P, Como S, Coppa S, Ikauniece A, Ruginis T, Jankowska E, Weslawski JM, Warzocha J, Gromisz S, Witalis B, Silva T, Ribeiro P, Fernandes De Matos VK, Sousa-Pinto I, Veiga P, Troncoso J, Guinda X, Juanes De La Pena JA, Puente A, Espinosa F, Pérez-Ruzafa A, Frost M, McNeill CL, Peleg O, Rilov G. 2016. Geographic patterns of biodiversity in European coastal marine benthos. *Journal of the Marine Biological Association of the United Kingdom* **97**: 496–505.
- Huston MA, Wolverton S. 2011. Regulation of animal size by eNPP, Bergmann's rule and related phenomena. *Ecological Monographs* **81**: 349–405.
- Hygum TL, Clausen LKB, Halberg KA, Jørgensen A, Møbjerg N. 2016. Tun formation is not a prerequisite for desiccation tolerance in the marine tidal tardigrade *Echiniscoides sigismundi*. *Zoological Journal of the Linnean Society* **178**: 907–911.
- James FC. 1970. Geographic size variation in birds and its relationship to climate. *Ecology* **51**: 365–390.
- Jenkins DG, Brescacin CR, Duxbury CV, Elliott JA, Evans JA, Grablow KR, Hillegass M, Lyon BN, Metzger GA, Olandese ML, Pepe D, Silvers GA, Suresch HN, Thompson TN, Trexler CM, Williams GE, Williams NC, Williams SE. 2007. Does size matter for dispersal distance? *Global Ecology and Biogeography* **16**: 415–425.
- Jenkins DG, Medley KA, Franklin RB. 2011. Microbes as a test of biogeographic principles. In: Fontaneto D, ed. *Biogeography of microscopic organisms: is everything small everywhere*. New York: Cambridge University Press, 309–323.
- Jones J, Gibb CE, Millard SC, Barg JJ, Girvan MK, Veit ML, Friesen VL, Robertson RJ. 2005. Multiple selection pressures generate adherence to Bergmann's rule in a Neotropical migratory songbird. *Journal of Biogeography* **32**: 1827–1833.
- Jørgensen A, Kristensen RM. 2001. A new tanarctid arthrotardigrade with buoyant bodies. *Zoologischer Anzeiger* **240**: 425–439.
- Jørgensen A, Møbjerg N. 2014. Notes on the cryptobiotic capability of the marine arthrotardigrades *Styraconyx haploceros* (Halechiniscidae) and *Batillipes pennaki* (Batillipedidae) from the tidal zone in Roscoff, France. *Marine Biology Research* **11**: 214–217.
- Kaczmarek Ł, Bartels PJ, Roszkowska M, Nelson DR. 2015. The zoogeography of marine Tardigrada. *Zootaxa* **4037**: 1–189.
- Kamilar JM, Cooper N. 2013. Phylogenetic signal in primate behaviour, ecology and life history. *Philosophical Transactions of the Royal Society B: Biological Sciences* **368**: 20120341.
- Kinchin I. 1994. *The biology of tardigrades*. London: Portland Press.
- Kristensen RM, Hallas, TE 1980. The tidal genus *Echiniscoides* and its variability, with erection of Echiniscoididae fam. n. (Tardigrada). *Zoologica Scripta* **9**: 113–127.
- Kristensen RM, Mackness BS. 2000. First record of the marine tardigrade genus *Batillipes* (Arthrotardigrada: Batillipedidae) from South Australia with a description of a new species. *Records of the South Australia Museum* **33**: 73–87.
- Lefort S, Aumont O, Bopp L, Arsouze T, Gehlen M, Maury O. 2015. Spatial and body-size dependent response of marine pelagic communities to projected global climate change. *Global Change Biology* **21**: 154–164.
- Lindsey CC. 1966. Body sizes of poikilotherm vertebrates at different latitudes. *Evolution* **20**: 456–465.
- Lindstedt SL, Boyce MS. 1985. Seasonality, fasting endurance, and body size in mammals. *The American Naturalist* **125**: 873–878.
- Makarieva AM, Gorshkov VG, Li BL. 2005. Temperature-associated upper limits to body size in terrestrial poikilotherms. *Oikos* **111**: 425–436.
- McInnes SJ. 1994. Zoogeographic distribution of terrestrial/freshwater tardigrades from current literature. *Journal of Natural History* **28**: 257–352.
- McNab BK. 2010. Geographic and temporal correlations of mammalian size reconsidered: a resource rule. *Oecologia* **164**: 13–23.
- Meiri S. 2011. Bergmann's Rule – what's in a name? *Global Ecology and Biogeography* **20**: 203–207.
- Merckx T, Souffreau C, Kaiser A, Baardsen LF, Backeljau T, Bonte D, Brans KI, Cours M, Dahirel M, Debortoli N, De Wolf K, Engelen JMT, Fontaneto D, Gianuca AT, Govaert L, Hendrickx F, Higuti J, Lens L, Martens K, Matheve H, Matthysen E, Piano E, Sablon R, Schön I, Van Doninck K, De Meester L, Van Dyck H. 2018. Body-size shifts in aquatic and terrestrial urban communities. *Nature* **558**: 113–116.
- Møbjerg N, Kristensen RM, Jørgensen A. 2016. Data from new taxa infer *Isoechiniscoides* gen. nov. and increase the phylogenetic and evolutionary understanding of echiniscoidid tardigrades (Echiniscoidea: Tardigrada). *Zoological Journal of the Linnean Society* **178**: 804–818.
- Moran AL, Woods HA. 2012. Why might they be giants? Towards an understanding of polar gigantism. *The Journal of Experimental Biology* **215**: 1995–2002.
- Munkemuller T, Lavergne S, Bzeznik B, Dray S, Jombart T, Schiffrers K, Thuiller W. 2012. How to measure and test phylogenetic signal. *Methods in Ecology and Evolution* **3**: 743–756.
- Narayanaswamy BE, Coll M, Danovaro R, Davidson K, Ojaveer H, Renaud PE. 2013. Synthesis of knowledge on marine biodiversity in European seas: from census to sustainable management. *PLoS ONE* **8**: e58909.
- Nelson DR, Guidetti R, Rebecchi L. 2015. Chapter 17, Phylum Tardigrada. In: Thorp J, Rogers DC, eds. *Thorp and Covich's freshwater invertebrates*. London: Academic Press, 347–380.
- Ohlberger J. 2013. Climate warming and ectotherm body size – from individual physiology to community ecology. *Functional Ecology* **27**: 991–1001.
- Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W. 2013. *Caper: comparative analyses of phylogenetics and evolution in R. R package version 0.5.2*.

- Pagel M. 1999.** Inferring the historical patterns of biological evolution. *Nature* **401**: 877–884.
- Peck LS, Harper EM. 2010.** Variation in size of living articulated brachiopods with latitude and depth. *Marine Biology* **157**: 2205–2213.
- Perry E, Miller WR, Kaczmarek Ł. 2019.** Recommended abbreviations for the names of genera of the phylum Tardigrada. *Zootaxa* **4608**: 145–154.
- Peters RH. 1983.** *The ecological implications of body size*. Cambridge: Cambridge University Press.
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. 2014.** *Nlme: linear and nonlinear mixed effects models. R package version 3.1-118*.
- Poulin R. 1996.** The evolution of body size in the Monogenea: the role of host size and latitude. *Canadian Journal of Zoology* **74**: 726–732.
- R Core Team. 2014.** *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Ramazzotti G, Maucci W. 1983.** Il Phylum Tardigrada. *Memorie dell'Istituto Italiano di Idrobiologia* **41**: 1–1012.
- Rasconi S, Gall A, Winter K, Kainz MJ. 2015.** Increasing water temperature triggers dominance of small freshwater plankton. *PLoS ONE* **10**: e0140449.
- Ray C. 1960.** The application of Bergmann's and Allen's Rules to the poikilotherms. *Journal of Morphology* **106**: 85–108.
- Renaud-Mornant, J. 1989.** Espèces nouvelles de Florarctinae de l'Atlantique Nord-Est et du Pacifique Sud (Tardigrada, Arthrotardigrada). *Bulletin du Muséum National d'Histoire Naturelle*, Paris, 4e ser., **11** (Section A, No 3): 571–592.
- Reynolds CS. 1984.** *The ecology of freshwater phytoplankton*. Cambridge: Cambridge University Press.
- Reynolds CS. 1994.** *The role of fluid motion in the dynamics of phytoplankton in lakes and rivers*. London: Blackwell Scientific.
- Rundle SD, Bilton DT, Foggo A. 2007.** By wind, wings or water: body size, dispersal and range size in aquatic invertebrates. In: Hildrew AG, Raffaelli DG, Edmonds-Brown R, eds. *Body size: the structure and function of aquatic ecosystems*. Cambridge: Cambridge University Press, 186–209.
- Schmidt-Nielsen K. 1984.** *Scaling: why is animal size so important?* Cambridge: Cambridge University Press.
- Schultze, M. 1865.** Echiniscus Sigismundi, ein Arctiscoide der Nordsee. *Archiv für mikroskopische Anatomie* **1**: 428–436.
- Smith CR, Drazen J, Mincks SL. 2006.** Deep-sea biodiversity and biogeography: perspectives from the abyss. In: *International Seabed Authority Seamount Biodiversity Symposium*, 1–13.
- Sommer U, Peter KH, Genitsaris S, Moustaka-Gouni M. 2017.** Do marine phytoplankton follow Bergmann's rule *sensu lato*? *Biological Reviews of the Cambridge Philosophical Society* **92**: 1011–1026.
- Stevenson RD. 1985.** Body size and limits to the daily range of body temperature in terrestrial ectotherms. *The American Naturalist* **125**: 102–117.
- Van Voorhies WA. 1996.** Bergmann size clines: a simple explanation for their occurrence in ectotherms. *Evolution* **50**: 1259–1264.
- Vicente F, Bertolani R. 2013.** Considerations on the taxonomy of the phylum Tardigrada. *Zootaxa* **3626**: 245–248.
- Vinarski MV. 2014.** On the applicability of Bergmann's rule to ectotherms: the state of the art. *Biology Bulletin Reviews* **4**: 232–242.
- Warwick RM. 2007.** Body size and diversity in marine systems. In: Hildrew AG, Raffaelli DG, Edmonds-Brown R, eds. *Body size: the structure and function of aquatic ecosystems*. Cambridge: Cambridge University Press, 210–224.
- Waters JM. 2008.** Driven by the West Wind Drift? A synthesis of southern temperate marine biogeography, with new directions for dispersalism. *Journal of Biogeography* **35**: 417–427.
- Watt C, Mitchell S, Salewski V. 2010.** Bergmann's rule; a concept cluster? *Oikos* **119**: 89–100.
- Westberry T, Behrenfeld MJ, Siegel DA, Boss E. 2008.** Carbon-based primary productivity modeling with vertically resolved photoacclimation. *Global Biogeochemical Cycles* **22**: GB2024. doi: 10.1029/2007GB003078.
- de Wit R, Bouvier T. 2006.** 'Everything is everywhere, but, the environment selects'; what did Baas Becking and Beijerinck really say? *Environmental Microbiology* **8**: 755–758.
- Zeveloff SI, Boyce MS. 1988.** Body size patterns in North American mammal faunas. In: Boyce MS, ed. *Evolution of life histories of mammals: theory and pattern*. New Haven: Yale University Press, 123–146.
- Zohary T, Fishbein T, Shlichter M, Naselli-Flores L. 2017.** Larger cell or colony size in winter, smaller in summer – a pattern shared by many species of Lake Kinneret phytoplankton. *Inland Waters* **7**: 200–209.
- Zuur AF, Ieno EN, Walker NJ, Savelieve AA. 2009.** *Mixed effects models and extensions in ecology with R*. New York, NY: Springer.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Phylogenetic relationships between the 209 taxonomic units at species and subspecies level used for the analyses. This phylogeny was modified from Fujimoto *et al.* (2016) and Møbjerg *et al.* (2016). A few unresolved taxa (*Neostygartus*, *Neoarctus*, *Euclavarctinae*, *Quisartus* and *Anisonyches*) were positioned based on our best guess from existing literature on overall morphological similarities.

Table S1. Results of the comparison between generalized least squares models including non-spatial and various spatial structures, testing the effect of latitude (absolute and quadratic values), number of records, number of

papers, and subdivision into six main geographical areas (West Atlantic Ocean, East Atlantic Ocean, Indian Ocean, West Pacific Ocean, Central Pacific Ocean and East Pacific Ocean) on species richness at four different spatial scales (grids at 10, 5, 2 and 1°). For each spatial scale, the Akaike information criterion (AIC) values and the degrees of freedom of each model are reported; the lowest AIC value for each set of models is reported in bold. The results of a likelihood ratio test between the non-spatial model and the model with the lowest AIC value is reported with the value of the likelihood ratio and the *P*-value.

Table S2. Results of the analyses of latitudinal gradients in species richness, accounting for the number of records, number of papers and subdivision into six main geographical areas, at spatial scales with square grids at 10, 5 and 2°. Results of linear models (LMs) are reported because no spatial structure was detected at any scale (Supporting Information, Table S1). The table reports output as a type II test ANOVA table, with the *F*-value, *P*-value, partial R^2 (lmg) and relative importance (RI) for each explanatory variable. The sum of the total of the partial R^2 (lmg) represents the adjusted R^2 of each model. Significant *P*-values with an α -level = 0.001 are reported in bold.

Table S3. Results of the comparison between generalized least squares models including non-spatial and various spatial structures, testing the effect of latitude (absolute and quadratic values), species richness and subdivision into six main geographical areas (West Atlantic Ocean, East Atlantic Ocean, Indian Ocean, West Pacific Ocean, Central Pacific Ocean and East Pacific Ocean) on median body size at four different spatial scales (grids at 10, 5, 2 and 1°). For each spatial scale, the Akaike information criterion (AIC) values and the degrees of freedom of each model are reported; the lowest AIC value for each set of models is reported in bold. The results of a likelihood ratio test between the non-spatial model and the model with the lowest AIC value are reported with the value of the likelihood ratio and the *P*-value.

Table S4. Results of the analyses of latitudinal gradients in median, minimum and maximum body size, accounting for absolute and quadratic forms of latitude, species richness and subdivision into six main geographical areas, at three spatial scales, with square grids at 10, 5 and 2°. For median values, results of linear models (LMs) are reported for 10°, and results of generalized least squares (GLS) with spherical (for 5 and 2°) spatial structure. For minimum values, the results of LMs are reported for 10°, and results of GLS with spherical spatial structure (for 5 and 2°). For maximum values, results of LMs are reported for 10°, and results of GLS with spherical (for 5 and 2°) are reported depending on the best spatial structure found for each model. The table reports output as a type II test ANOVA table with *F*-value for LMs and χ^2 for GLS models, *P*-value, partial R^2 (lmg) for LMs, and relative importance (RI) for each explanatory variable. Significant *P*-values with α -level = 0.001 are reported in bold.

Table S5. Results of the analyses of latitudinal gradients in median body size for the Northern (A) and the Southern Hemisphere (B), accounting for absolute and quadratic forms of latitude, species richness and subdivision into six main geographical areas, at four spatial scales, with square grids at 10, 5, 2 and 1°. Results of linear models (LMs) are reported for all the Southern Hemisphere and for the Northern Hemisphere at 10°, whereas for the Northern Hemisphere results are reported of generalized least squares (GLS) with spherical (for 5°), Gaussian (for 2°) and ratio (for 1°) spatial structure, depending on the best spatial structure found for each model. The table reports model estimate, *t*-value, *P*-value, partial R^2 (lmg) for LMs, and relative importance (RI) for each explanatory variable. Significant *P*-values with an α -level = 0.001 are reported in bold.

Table S6. Phylogenetic signal in body size, number of records and latitudinal metrics. Pagel's λ and Blomberg's *K* are reported. Values close to zero mean no phylogenetic signal, whereas values close to one mean that a phylogenetic signal is present.

Table S7. Results of the phylogenetic generalized least squares models to test the effect of body size and number of records on latitudinal metrics such as minimum, maximum, median and range in their absolute and actual values.

Table S8. Results of the comparison between generalized least squares models including non-spatial and various spatial structures, testing the effect of latitude (absolute and quadratic values), number of records, number of papers and subdivision into six main geographical areas (West Atlantic Ocean, East Atlantic Ocean, Indian Ocean, West Pacific Ocean, Central Pacific Ocean and East Pacific Ocean) on the species richness of Heterotardigrada at four different spatial scales (grids at 10, 5, 2 and 1°). For each spatial scale, the Akaike information criterion (AIC) values and the degrees of freedom of each model are reported; the lowest AIC value for each set of models is reported in bold. The results of a likelihood ratio test between the non-spatial model and the model with the lowest AIC value are reported with the value of the likelihood ratio and the *P*-value.

Table S9. Results of the analyses of latitudinal gradients in species richness of Heterotardigrada, accounting for the number of records, number of papers and subdivision into six main geographical areas, at four spatial scales, with square grids at 10, 5, 2 and 1°. Results of linear models (LMs) are reported because no spatial structure was detected at any scale (Supporting Information, Table S13). The table reports the model estimate, *t*-value, *P*-value,

partial R^2 (lmg) and relative importance (RI) for each explanatory variable. The sum of the total of the partial R^2 (lmg) represents the adjusted R^2 of each model. Significant P -values with an α -level = 0.001 are reported in bold. **Table S10.** Results of the comparison between generalized least squares models including non-spatial and various spatial structures, testing the effect of latitude (absolute and quadratic values), species richness and subdivision into six main geographical areas (West Atlantic Ocean, East Atlantic Ocean, Indian Ocean, West Pacific Ocean, Central Pacific Ocean and East Pacific Ocean) on median body size for Heterotardigrada at four different spatial scales (grids at 10, 5, 2 and 1°). For each spatial scale, the Akaike information criterion (AIC) values and the degrees of freedom of each model are reported; the lowest AIC value for each set of models is reported in bold. The results of a likelihood ratio test between the non-spatial model and the model with the lowest AIC value are reported, with the value of the likelihood ratio and the P -value.

Table S11. Results of the analyses of latitudinal gradients in median body size of Heterotardigrada, accounting for absolute and quadratic forms of latitude, species richness and subdivision into six main geographical areas, at four spatial scales, with square grids at 10, 5, 2 and 1°. Results of linear models (LMs) are reported for 10 and 5°, and results of generalized least squares (GLS) models with spherical (for 2°) and ratio (for 1°) spatial structure are reported depending on the best spatial structure found for each model (Supporting Information, Table S15). The table reports the model estimate, t -value, P -value, partial R^2 (lmg) for LMs, and relative importance (RI) for each explanatory variable. Significant P -values with an α -level = 0.001 are reported in bold.

Table S12. Results of the analyses of latitudinal gradients in minimum body size of Heterotardigrada, accounting for absolute and quadratic forms of latitude, species richness and subdivision into six main geographical areas, at four spatial scales, with square grids at 10, 5, 2 and 1°. Results of linear models (LMs) are reported for 10, 5 and 1°, and results of generalized least squares (GLS) models with spherical spatial structure are reported for 2°, depending on the best spatial structure found for each model (Supporting Information, Table S15). The table reports the model estimate, t -value, P -value, partial R^2 (lmg) for LMs, and relative importance (RI) for each explanatory variable. Significant P -values with α -level = 0.001 are reported in bold.

Table S13. Results of the analyses of latitudinal gradients in minimum body size of Heterotardigrada for the Northern Hemisphere, accounting for absolute and quadratic forms of latitude, species richness and subdivision into six main geographical areas, at four spatial scales, with square grids at 10, 5, 2 and 1°. Results of linear models (LMs) are reported for the Northern Hemisphere at 10, 5 and 1°, and results of generalized least squares (GLS) models with Gaussian spatial structure for 2°, depending on the best spatial structure found for each model. The table reports the model estimate, t -value, P -value, partial R^2 (lmg) for LMs, and relative importance (RI) for each explanatory variable. Significant P -values with an α -level = 0.001 are reported in bold.

Table S14. Results of the analyses of latitudinal gradients in maximum body size of Heterotardigrada, accounting for absolute and quadratic forms of latitude, species richness and subdivision into six main geographical areas, at four spatial scales, with square grids at 10, 5, 2 and 1°. Results of linear models (LMs) are reported for 10 and 5°, and results of generalized least squares (GLS) models with spherical (for 3°) and Gaussian (for 1°) spatial structure are reported, depending on the best spatial structure found for each model (Supporting Information, Table S15). The table reports the model estimate, t -value, P -value, partial R^2 (lmg) for LMs, and relative importance (RI) for each explanatory variable. Significant P -values with an α -level = 0.001 are reported in bold.

Table S15. Results of the analyses of latitudinal gradients in maximum body size of Heterotardigrada for the Northern Hemisphere, accounting for absolute and quadratic forms of latitude, species richness and subdivision into six main geographical areas, at four spatial scales, with square grids at 10, 5, 2 and 1°. Results of linear models (LMs) are reported for the Northern Hemisphere at 10 and 5°, and results of generalized least squares (GLS) models with spherical (for 2°) and Gaussian (for 1°) spatial structure, depending on the best spatial structure found for each model. The table reports the model estimate, t -value, P -value, partial R^2 (lmg) for LMs, and relative importance (RI) for each explanatory variable. Significant P -values with an α -level = 0.001 are reported in bold.