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Beyond Bergmann's rule: size–latitude relationships in marine Bivalvia world-wide

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ABSTRACT

Aim Variations in body size are well established for many taxa of endotherms and ectotherms, but remain poorly documented for marine invertebrates. Here we explore how body size varies with latitude, temperature and productivity for a major marine invertebrate class, the Bivalvia.

Location Continental shelves world-wide.

Methods We used regression models to assess univariate relationships between size and latitude as well as multivariate relationships between size, latitude and environmental parameters (mean and seasonality in temperature and mean productivity). The dataset consisted of 4845 species in 59 families from shelf depths at all latitudes in the Pacific and Atlantic oceans. We also used Blomberg's *K* to assess whether size–latitude relationships show phylogenetic signal, and test whether functional groups based on feeding mode, substrate relationships, mobility and fixation can account for observed size–latitude trends.

Results Size–latitude trends are taxonomically and geographically common in bivalves, but vary widely in sign and strength – no simple explanations based on environmental parameters, phylogeny or functional group hold across all families. Perhaps most importantly, we found that the observed trends vary considerably between hemispheres and among coastlines.

Main conclusions Broadly generalizable macroecological patterns in inter-specific body size may not exist for marine invertebrates. Although size–latitude trends occur in many bivalve lineages, the underlying mechanisms evidently differ among regions and/or lineages. Fully understanding macroecological patterns requires truly global datasets as well as information about the evolutionary history of specific lineages and regions.

Keywords

Bivalves, body size, continental shelves, ecogeographic rules, size–latitude trends.

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INTRODUCTION

Macroecological patterns in body size are well documented for a wide variety of animal taxa, including endotherms and ectotherms in terrestrial, aquatic and marine habitats world-wide (Lindsey, 1966; Mousseau, 1997; Partridge & Coyne, 1997; Blackburn *et al.*, 1999; Ashton, 2002a; Belk & Houston, 2002; Ashton & Feldman, 2003; Freckleton *et al.*, 2003; Chown & Gaston, 2010). Such patterns were first codified in Bergmann's rule, which posits that body size increases with latitude

(Bergmann, 1848; reviewed Partridge & Coyne, 1997; Blackburn *et al.*, 1999; Ashton & Feldman, 2003; Freckleton *et al.*, 2003; Meiri, 2011). Although Bergmann restricted his comments to mammals, similar trends have been documented for numerous ectothermic taxa (Ray, 1960; Partridge & Coyne, 1997) including many insect groups (Arnett & Gotelli, 2003; Chown & Gaston, 2010), turtles (Ashton & Feldman, 2003), some salamanders (Ashton, 2002b), some anurans (Ashton, 2002b; Olalla-Tárraga & Rodríguez, 2007), marine fishes (Lindsey, 1966; Belk & Houston, 2002), copepods (Lonsdale & Levinton, 1985), isopods

(Cardoso & Defeo, 2003) and mole crabs (Defeo & Cardoso, 2002). Converse Bergmann trends, in which size decreases with latitude, are also frequently reported in ectotherms, e.g. in many other insect groups (Mousseau, 1997; Chown & Gaston, 2010), other salamanders (Olalla-Tárraga & Rodríguez, 2007), freshwater fishes (Belk & Houston, 2002) and European lizards (Olalla-Tárraga & Rodríguez, 2007). While both Bergmann and converse Bergmann trends are clearly common, comparison among studies is complicated by differing taxonomic levels (Blackburn *et al.*, 1999). Although Bergman's rule was originally defined inter-specifically (Blackburn *et al.*, 1999), it has commonly been applied to populations within a single species, and the mechanisms thus far implicated in size–latitude trends are primarily limited to intra-specific scales – no general mechanism accounting for inter-specific size–latitude patterns has been suggested. For ectotherms, intra-specific size–latitude trends are commonly thought to reflect the physiology of growth and development. For example, the temperature–size rule suggests that Bergmann trends arise from crossing growth and development trajectories – if development accelerates more rapidly than somatic growth as temperature increases, smaller adult body size can result at high temperatures (Chown & Gaston, 2010; Arendt, 2011). Some evidence also suggests that selection for starvation resistance can produce intra-specific Bergmann trends – if larger-bodied individuals tolerate seasonal fluctuations in resource availability better than smaller-bodied individuals, selection may favour larger-bodied populations at high latitude (Kendeigh, 1969; Erlinge, 1987; Arnett & Gotelli, 2003). Resource availability can also directly control adult body size, potentially explaining the converse Bergmann clines seen in some species (e.g. insects that grow larger at low latitude may have a more abundant or higher quality food supply than higher-latitude conspecifics) (Erlinge, 1987; Conover, 1990; Chown & Gaston, 2010; Arnett & Gotelli, 2003). Such mechanisms, all of which apply to populations within species, can produce significant correlations between body size, temperature and/or resource availability (or some proxy thereof, i.e. productivity) among conspecific populations. Similar correlations will only be observed inter-specifically if most species within a family or genus are governed by the same mechanism, which may or may not be the case. Alternatively, inter-specific size–latitude trends may arise indirectly, e.g. if body size is genetically linked to other traits that directly respond to some correlate of latitude (Blackburn *et al.*, 1999), or to traits that promote regional differences in diversification within and among clades (Jablonski, 2010).

If inter-specific size–latitude trends in ectotherms reflect species responses to environmental parameters such as temperature and productivity, then consistent correlations would be expected between those parameters and body sizes among clades, or within clades among oceans. Body size, however, is influenced by complex ecological and evolutionary tradeoffs between growth, resource availability, reproduction, predation, longevity and any number of other factors in addition to historical events, so that inter-specific patterns may fail to be simple extensions of intra-specific processes. To explore these issues, we

analysed inter-specific size–latitude, size–temperature and size–productivity trends for a major class of marine invertebrates, the Bivalvia, in coastal oceans world-wide.

Bivalves are important components of marine benthic ecosystems, occurring at all latitudes and all depths in all the world's oceans (Bieler & Mikkelsen, 2006; Krug *et al.*, 2009). By focusing on marine invertebrates, this study fills a gap in our understanding of macroecological patterns in body size, which have historically been biased towards terrestrial and/or vertebrate systems. Bivalves provide an ideal system for studying size variation, spanning four orders of magnitude from less than 1 mm to over 1 m in shell length. Using a comprehensive database of geographic distributions and body sizes of bivalve species world-wide, we quantitatively assess size–latitude trends for 59 families. We evaluate whether bivalve size–latitude trends covary with temperature and primary productivity in the sea. Furthermore, we assess whether size trends show patterns within functional groups based on feeding mode, substrate relationship, fixation and mobility. We also test for phylogenetic conservatism among families in size–latitude relationships. Finally, we evaluate whether all of these patterns are consistent across hemispheres and coastlines. The resulting analysis provides an assessment of size–latitude trends and their potential correlates for an unusually broad sample of ecologically important organisms.

METHODS

Body size data

Using a database of geographic occurrences and basic functional data for bivalves living at shelf depths world-wide (Krug *et al.*, 2008), we compiled body sizes and geographic occurrences of 4845 species from 59 families of bivalves (only families with more than six species of known body size were included). The resulting dataset consists of 39,280 individual species occurrences from 2277 shelf-depth localities world-wide (Fig. 1). Localities vary in spatial resolution from local (e.g. Shark Bay, Australia) to more regional scales (e.g. New South Wales) reflecting differential sampling of different parts of the world's oceans. Overall, the finest spatial resolution possible is 5° latitude/longitude, which is the scale used here. For each species, body size was taken as the single largest body size reported in the literature, calculated as the geometric mean of shell length and height on a log₂ scale [$\log_2(\text{length} \times \text{height})^{0.5}$]; this correlates well with biomass (Roy *et al.*, 2000a) and with other size metrics (Kosnik *et al.*, 2006). Using a single maximum size for each species ignores geographic variation in body size within species (which clearly exists and is ecologically meaningful), but: (1) we are primarily interested in inter-specific patterns; (2) intra-specific size data covering entire species' ranges are not available for the vast majority of bivalves in our database; and (3) for bivalves, the largest size reported for a species should correlate well to the largest size sampled from any given population (Kosnik *et al.*, 2006). Our size coverage represents 80–100% of all known species in the families analysed (mean 89%) and

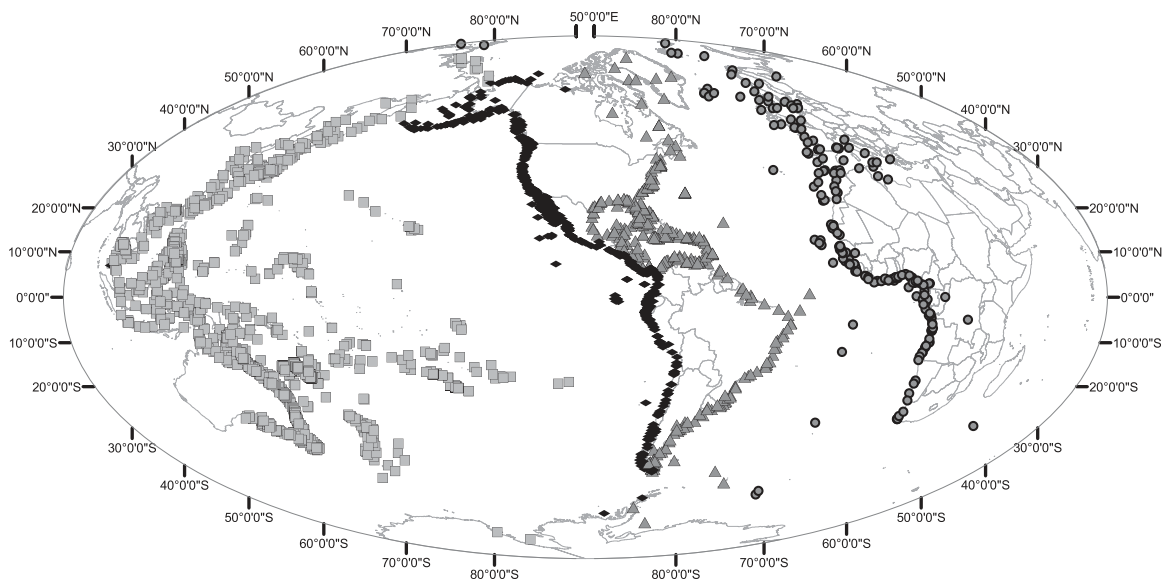


Figure 1 Localities used for each coastline (squares = western Pacific, diamonds = eastern Pacific, triangles = western Atlantic, circles = eastern Atlantic). World Hammer–Aitoff projection.

85–100% of all species in each of the major marine provinces (mean 94%) (see Tables S1 & S2 in Appendix S1 in the Supporting Information). Our sampling is thus both taxonomically and spatially extensive.

Latitudinal analyses

We calculated the median body size for each family in 5° latitudinal bands spanning each coastline, using the cells in which body size data exist to determine the longitudinal extent of each band, and quantified size–latitude trends using Gaussian linear regressions (R function ‘regress’, with a linear spatial covariance structure; Clifford & McCullagh, 2006). Median body size per 5° latitudinal band was modelled as a univariate linear function of latitude, conducting separate analyses for each of the major north–south coastlines: the West Atlantic, East Atlantic, West Pacific, and East Pacific. Spatial autocorrelation was addressed by specifying a covariance matrix based on the great circle distance between 5° bands, using the most landward edge of each band as longitude. Correcting for spatial autocorrelation is arguably not necessary for assessing Bergmann’s rule (which has always been defined solely in reference to latitude), nor indeed for any biogeographic analysis, given that the occurrence of taxa at multiple latitudes is due to biology rather than data-quality problems (Hawkins, 2011). In general, regression models with versus without a spatial covariance structure will have similar coefficients but different precision. Therefore, raw models with no spatial covariance are broadly consistent with the data presented here, but identify even more size–latitude trends as being significant. Given that many ecologists see spatial autocorrelation as a source of bias, we have chosen to err on the conservative side by including a spatial covariance structure in our models.

To account for the fact that some families show broadly symmetrical size patterns across the equator (either Bergmann or

converse Bergmann clines in both hemispheres) while others show monotonic patterns either increasing or decreasing across the equator (Fig. 2), we ran each model twice – once using raw latitudinal values and again using the absolute value of latitude. Families can also show significant pattern in one hemisphere but not the other, which can complicate the analysis of data from both hemispheres. Therefore, we additionally performed regressions in each hemisphere alone, using these results for families showing no pattern in body size over the full latitudinal range.

Environmental analysis

We calculated the annual mean and range (the difference between maximum and minimum monthly means) of both sea surface temperature (SST) and net primary productivity (NPP) for 5° × 5° grid cells world-wide. Bands spanning each coastline were then averaged for a given latitude, using the cells in which body size data exist to determine the longitudinal extent of each band. SST data were obtained from the UK Meteorological Office Hadley Centre (Rayner *et al.*, 2003; Met Office Hadley Centre 2006–2010). NPP data based on the vertically generalized production model (VGPM) using SeaWiFS and MODIS ocean colour chlorophyll estimates, SST and radiative forcing (Behrenfeld & Falkowski, 1997) were obtained from Guillaume Maze’s ocean productivity data site for the years 1997–2007 (Maze, 2011). Satellite-derived NPP estimates can be problematic in shelf-depth waters (Saba *et al.*, 2011), but *in situ* NPP data are not available at global scales. Nonetheless, estimates from ocean colour satellites correlate reasonably well with *in situ* datasets from coastal waters at the spatial scale we are interested in [$\text{Chl-}a_{\text{seaWiFS}} \sim (0.13 + 0.77) \times \text{Chl-}a_{\text{in-situ}}$; $R^2 = 0.77$, $\text{Chl-}a = \text{chlorophyll } a$; for SeaWiFS versus all available *in situ* data at sites shallower than 200 m world-wide; regression performed using NASA’s SeaBASS validation engine; Werdell *et al.*, 2003; NASA,

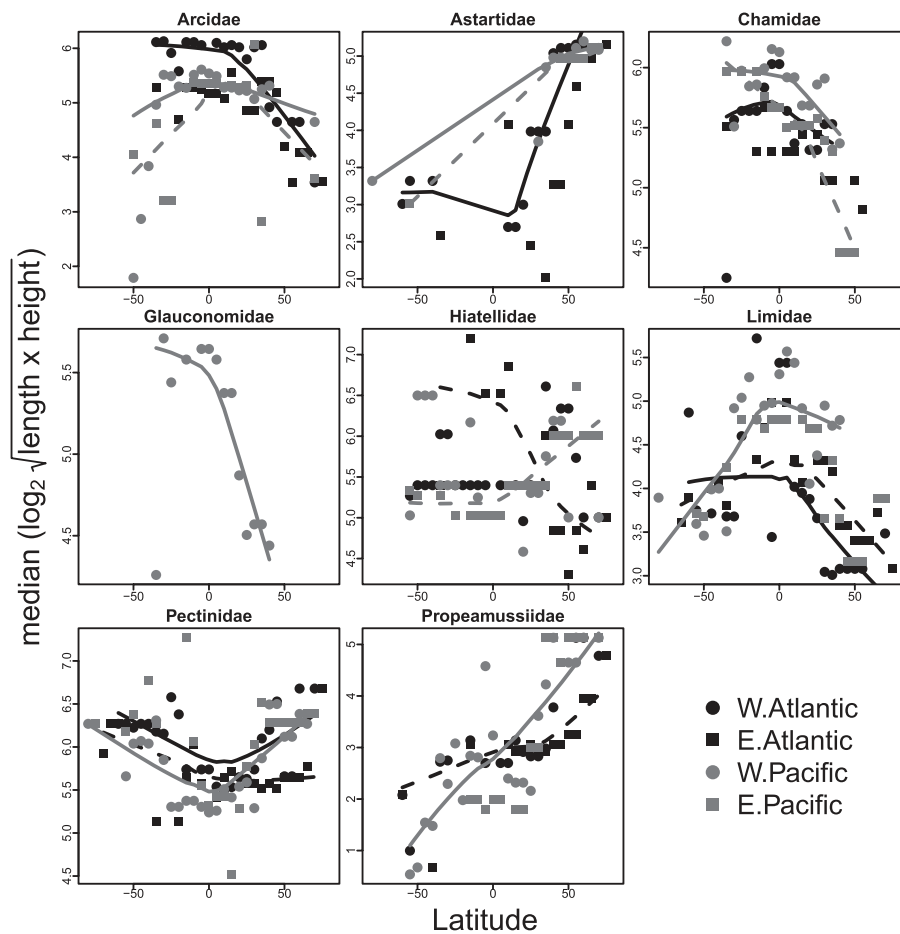


Figure 2 Body size versus latitude for eight marine bivalve families; plots for all 59 families are shown in Fig. S1 in Appendix S1. The number of species analysed for each family is given in Table S2 in Appendix S1, with total species richness and size coverage for each family. Points represent the median body size for all species occurring in each 5° latitudinal band on each coast (see legend). Lines are fitted Lowess curves not directly related to the regression analyses presented here; these lines are shown purely as visual aids to indicate trends in the raw data. Lines are only plotted for families showing significant correlations of size with latitude on a given coast. Solid black lines = West Atlantic, dashed black lines = East Atlantic, solid grey lines = West Pacific, dashed grey lines = East Pacific.

2011]. For each family on each coastline, the significant model terms were ranked using the *P*-values for each parameter, and patterns in how frequently each parameter was (1) significant or (2) the most significant were examined.

Using Gaussian linear multiple regressions, we modelled the family-level median body size per 5° latitudinal bin as a function of mean annual SST, annual range of SST, mean annual NPP and latitude for each of the major north–south coastlines. The annual range of NPP was not included, because it is strongly collinear with mean annual NPP. Spatial autocorrelation was addressed as described above. Each model was tested using raw latitude as well as the absolute value of latitude, keeping the model with the higher log-likelihood.

Functional analysis

If size trends are shaped by trade-offs involving resource acquisition or other aspects of functional biology and body size, then size trends might show patterns with functional groups. For

example, suspension-feeders are more directly tied to primary productivity in the water column than are deposit-feeders, carnivores and other trophic groups and so might show different latitudinal trends. Similarly, surface-dwelling, epifaunal taxa have often been held to exhibit different latitudinal trends from burrowing forms more buffered from environmental variation (see Roy *et al.*, 2000b). To evaluate such factors, we used non-metric multidimensional scaling (MDS) to assess the patterning of bivalve functional groups based on feeding mode, substrate relationship, mobility and fixation in a size–latitude multivariate space. A matrix of the median body size in each 5° latitudinal band (columns) for each family (rows) was used to generate a Euclidean distance matrix. Families were then plotted on the first two MDS axes, and points were coded by feeding mode (suspension feeding, deposit feeding, carnivorous, chemosymbiotic), substrate relationship (infaunal siphonate, infaunal asiphonate, epifaunal, boring, nestling, semi-infaunal or mixed within the family), fixation (byssate, cemented, unattached or mixed) and adult mobility (mobile, immobile or

mixed – species that swim or otherwise actively reposition themselves as adults are considered mobile). Separate MDS analyses were performed for each coastline.

The effects of family functional group membership on size–latitude trends were tested with permutational multivariate ANOVA (PMANOVA; 999 permutations) on the Euclidean distance matrix described above, grouping taxa by functional group (R function ‘adonis’ in the vegan package; Oksanen *et al.*, 2011). Within each coastline, four separate PMANOVAs were conducted, one for each axis of functional space (feeding mode, substrate relationship, mode of attachment and mobility).

Phylogenetic analysis

To assess whether size – latitude trends exhibit phylogenetic patterns, we mapped the first MDS axis scores from the size–latitude MDS (described above) onto a bivalve family-level phylogeny based on published trees (Fig. 3) (Giribet & Wheeler, 2002; Taylor *et al.*, 2007), with branch lengths estimated from the earliest fossil occurrence for each family (Krug *et al.*, 2010). We tested for phylogenetic signal among families in the size–latitude MDS scores using Blomberg’s *K* (Blomberg *et al.*, 2003). Separate analyses were conducted for each coastline. We also conducted a similar analysis using regression coefficients, with similar results. However, MDS scores are preferable because: (1) we feel that MDS points reflect the size–latitude relationship more directly than regression slopes, which are linear estimates of possibly more complicated patterns, and (2) some families have insufficient data for regressions on some coastlines, creating missing values, whereas the MDS points have no missing values.

RESULTS

Latitudinal patterns

Overall, significant size–latitude trends occur on at least one of the four major north–south coastlines (West Atlantic, East Atlantic, West Pacific and East Pacific) for 48 out of 59 families (Figs 2 & 3, Appendix 1, Fig. S1, Appendix S2). However, the patterns are heterogeneous – Bergmann and converse Bergmann trends both occur with equal frequency, and the mean slope is near 0 overall (means \pm SD by hemisphere/coast: south-west Atlantic 0.002 ± 0.012 ; north-west Atlantic -0.002 ± 0.016 ; south-east Atlantic -0.0001 ± 0.015 ; north-east Atlantic $.003 \pm 0.015$; south-west Pacific -0.003 ± 0.016 ; north-west Pacific 0.002 ± 0.019 ; south-east Pacific 0.004 ± 0.014 ; north-east Pacific 0.004 ± 0.013) (Fig. 4). Trends are somewhat more common in the Northern Hemisphere than the Southern Hemisphere (81 vs. 63), although most families that show trends do so in both hemispheres (only four families that occur in both hemispheres show trends limited to a single hemisphere; two in the north and two in the south) (Figs 2 & 3). Mixed trends (i.e. showing a Bergman trend in one hemisphere but a converse

Bergman trend in the other) are common, but occur about two-thirds as frequently as pure Bergmann or converse Bergmann trends. Families showing mixed trends are roughly evenly split in the direction of those trends (12 increasing vs. 10 decreasing from south to north). In general, within-family size–latitude trends are most common in the West Pacific, outnumbering trends on other coastlines two-to-one (49 in the West Pacific versus 25 in the East Atlantic, 19 in the West Atlantic, and 14 in the East Pacific). A majority of families (28 out of 48 with trends) show different trends on different coastlines, and trends are limited to a single hemisphere roughly one-third of the time. Despite this great heterogeneity, disparity between coastlines typically involves a trend in one coast/hemisphere that is simply absent from another coast/hemisphere. For example, the Arcidae shows converse Bergmann trends in both hemispheres of the East Pacific and in the northern Atlantic, but shows no pattern in the southern Atlantic. Families with diametrically opposed trends, e.g. the Myidae with a Bergman trend in the southern East Pacific and a converse Bergmann trend in the southern West Pacific, are a minority (11 of 48).

Environmental patterns

Family-level median body size correlates significantly with at least one environmental parameter in 10 to 36% of families, depending on the coastline (West Atlantic 34%, East Atlantic 28%, West Pacific 36%, East Pacific 10%). Latitude and mean annual SST have significant slopes with equal frequency (in 46 vs. 47 family/coast models, respectively), and are evenly divided as to which factor ranks as most important. Mean SST outranks latitude in 50% of models, latitude outranks SST in 45% of models, and the remaining 5% are ties (rank determined by *P*-value, counting across all coastlines). The annual range in SST and mean annual NPP are significant in 33 and 25 models, respectively, but outrank mean SST and/or latitude in fewer than 50% of cases. However, the annual range in SST is the most significant factor as frequently as mean annual SST in the East Atlantic. In summary, although environmental factors are correlated to body size patterns in some cases, an absence of correlation is far more common. No consistent patterns exist to suggest a strong relationship between any of the environmental parameters tested and the observed size–latitude patterns.

Functional patterns

Families exhibit significant clustering for some functional axes on some coastlines. Mobile versus immobile families cluster separately in the size–latitude multivariate space in the West Atlantic ($P = 0.009$) and East Pacific ($P = 0.009$). Feeding modes cluster separately in the West Pacific ($P = 0.004$) and, marginally, in the East Atlantic ($P = 0.09$), and substrate relationships cluster marginally significantly in the West Atlantic ($P = 0.07$) (Fig 5 & Fig. S2 in Appendix S1). These patterns in the size–latitude multivariate space correspond to differences in the relative proportion of families exhibiting positive, negative or mixed size–

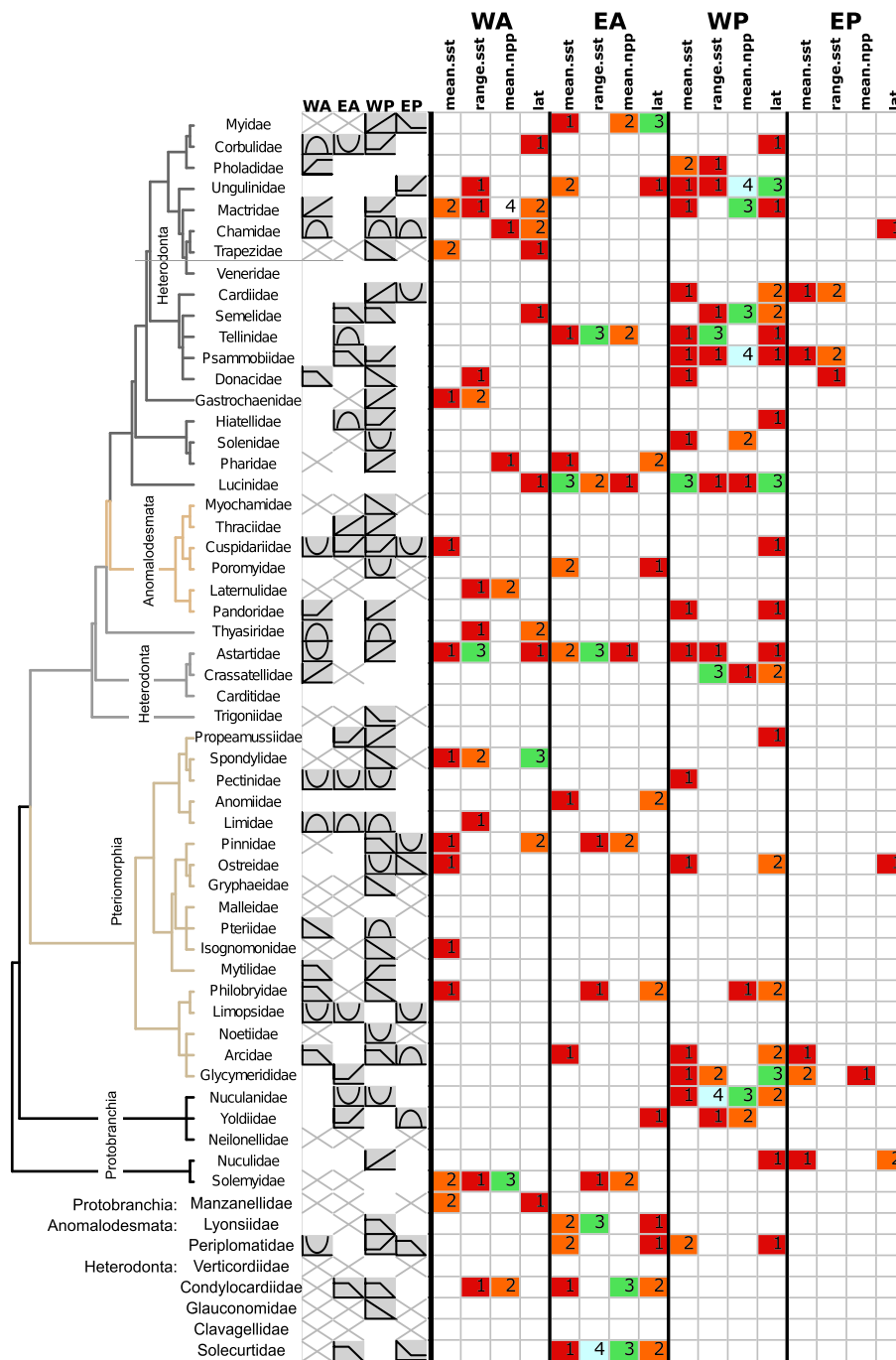


Figure 3 Phylogenetic distribution of body size trends with latitude and environmental parameters in marine Bivalvia. The cladogram is based on combined phylogenies from Giribet & Wheeler (2002), based on 183 morphological characters, 18S and 28S rRNA, and cytochrome *c* oxidase subunit I sequences, and Taylor *et al.* (2007), based on 18S and 28S rRNA sequences. Only families analysed in this study are included. The precise phylogenetic position is not known for eight of the families analysed; these are shown below the tree. Families with significant univariate relationships with latitude are indicated by heuristic plots showing the qualitative shape of size trends on each coastline (West Atlantic = WA, East Atlantic = EA, West Pacific = WP, East Pacific = EP). Crosses indicate that the family does not occur over an appreciable portion of a given coastline. Coloured squares indicate the rank of each factor – mean annual sea surface temperature (SST), annual range of SST, mean annual net primary productivity (NPP) and latitude – in multiple regressions, based on the *P*-value of the *t*-test on the slope for each parameter. The strongest predictors are indicated (for the online article) by red squares, followed by orange, green and blue (labelled 1 to 4, respectively, for the print publication). White indicates that the parameter was not significant. Ties share a colour. While median body size commonly does correlate with each of the predictors, there are no consistent patterns in which environmental parameter is most important, and latitude is often a better predictor than any environmental variables.

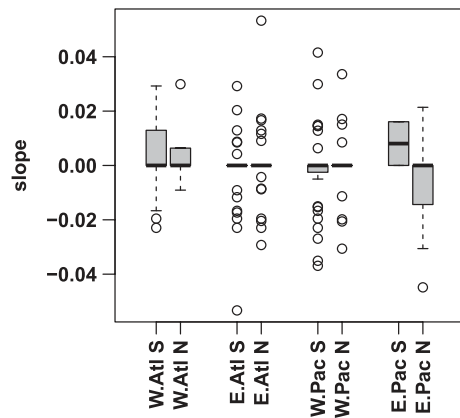


Figure 4 Boxplots showing the distributions of size–latitude slopes for each hemisphere of each coastline. The y -axis indicates coefficients from regression models for median body size versus latitude, with a spatial covariance structure based on great circle distances. Atl = Atlantic, Pac = Pacific.

latitude trends. For example, mobile versus immobile families show varying proportions of Bergmann, converse Bergmann and mixed trends on each of the four coastlines; however, there is no consistent pattern across coastlines. In the West Atlantic, immobile families show primarily converse Bergmann with some mixed trends, while mobile families show all three trends; in contrast, eastern Pacific immobile families show all three trends and mobile families show only two (Bergmann and converse Bergmann) (Fig. 5). Similarly, families with different substratum relationships show significant patterning in the West Atlantic, reflecting the lack of converse Bergmann trends among infaunal asiphonate families on that coastline. However, infaunal asiphonate families do show converse Bergmann clines in the East Atlantic and the West Pacific (Fig. S3 in Appendix S1). Finally, feeding modes show significant patterns in the West Pacific size–latitude space, reflecting the higher frequency of Bergmann trends among deposit feeders versus suspension feeders, and the lack of converse Bergmann trends among carnivores. However, deposit feeders show only converse Bergmann trends in the East Pacific and show no patterns in the West Atlantic. Overall, then, size–latitude trends are unevenly distributed among functional groups within a coastline in some cases, but no global patterns consistently linking particular functional groups to particular size–latitude trends are apparent.

Phylogenetic patterns

Trends are scattered across the bivalve phylogeny, showing few consistent patterns in the shape of size–latitude trends for related families (Figs 2 & 3). Sister families commonly show inconsistent or contradictory trends. For example, the Spondyliidae shows a monotonic decrease from north to south in the West Pacific, while the Pectinidae shows classical Bergmann trends there. Similarly, the Ostreidae shows converse Bergmann trends in the West Pacific, while the Gryphaeidae show a mono-

tonic decrease from south to north there. The first axis of the size–latitude ordination space showed no phylogenetic patterning among families on any coastline (West Atlantic $K = 0.11$, $P = 0.37$; East Atlantic $K = 0.18$, $P = 0.12$; West Pacific $K = 0.09$, $P = 0.40$; East Pacific $K = 0.09$, $P = 0.62$).

DISCUSSION

Bivalve size–latitude trends are taxonomically and geographically common, but also immensely variable. Significant size–latitude relationships occur in 81% of the bivalve families investigated, but Bergmann and converse Bergmann trends occur with roughly equal frequency. In fact, families showing a mixture of Bergmann and converse Bergmann clines on different coastlines and/or in different hemispheres are in the majority by far. Trends are most common in the Northern Hemisphere and in the western Pacific (Fig. 3). Our results also show that neither temperature nor productivity provide a general explanation of size–latitude trends across all families. Furthermore, size–latitude trends are not strongly constrained by phylogeny or functional mode.

Given the strong variations in shape, spatial distribution and phylogenetic distribution of bivalve size trends, it is tempting to attribute them to sampling biases. While some regions of the world still remain poorly sampled (e.g. the Southern Ocean or the West African shelf), our data are spatially and taxonomically extensive enough to identify trends where they exist. Thus, it is unlikely that improved sampling would fill in so much new data that a consistent global pattern would emerge where we currently find significant but highly heterogeneous trends. Sampling can also be biased by body size, and small bivalves are likely to be undersampled relative to large ones in today's oceans just as they are in the fossil record (Valentine *et al.*, 2006). This sampling bias can make the smallest members of a family appear less widespread than they truly are, distorting observed latitudinal trends in size. However, several factors suggest that such bias is unlikely to substantially influence our analyses. (1) The families included here are unlikely to harbour numerous undiscovered small species, given that most of them are well-studied. More importantly, size is conserved at the family level for bivalves (not shown), suggesting that undescribed species will be similar in size to the rest of the family. (2) One of the smallest-sized families, the Condylocardiidae (1–4 mm shell length), is represented at all latitudes in our dataset, despite its small size, suggesting that even small species are spatially well-represented in our data. (3) Finally, more recently described bivalves are not disproportionately small and there is no strong relationship between body size and date of description for bivalves (Fig. S4, Mikkelsen, 2011), in marked contrast to several vertebrate and insect groups (Blackburn & Gaston, 1994).

If size–latitude relationships are related to ecological characteristics such as feeding mode or substrate relationships, then ecologically similar families should exhibit similar trends. Again, the data are not consistent with this hypothesis (Fig. 5). Groups of ecologically similar families show diverse trends, and groups of families with similar trends are ecologically diverse.

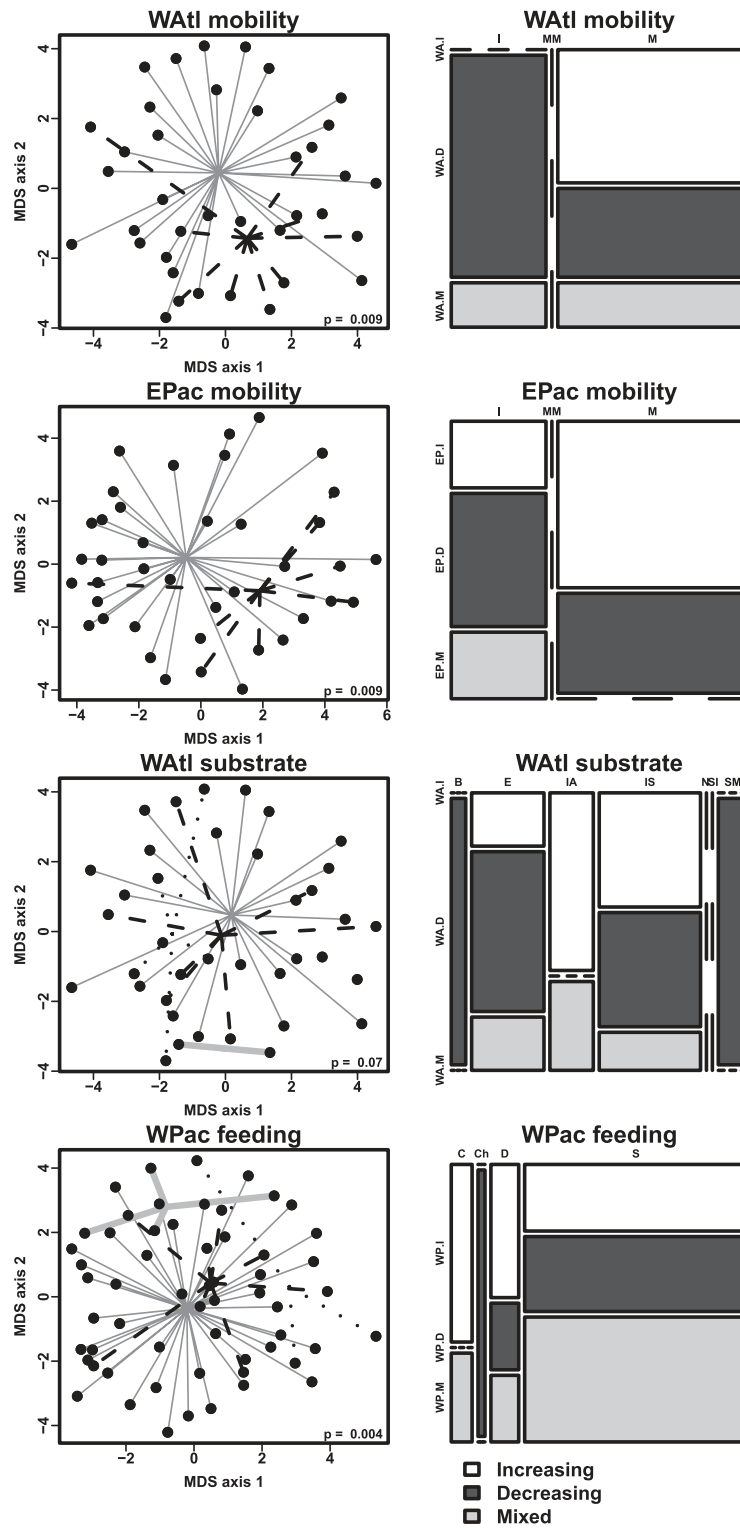


Figure 5 Multidimensional scaling (MDS) of the size–latitude multivariate space, showing significant clustering by functional groups. Each point is a family, and lines connect families within a single functional group. *P*-values are for permutational multivariate ANOVAs conducted on the Euclidean distance matrix used for the MDS analysis; these test for differences in size–latitude patterning among the categories in each functional group. MDS plots for all coasts and functional axes are shown in Fig. S2 in Appendix S1. For mobility, thin grey lines = mobile and black dashed lines = immobile. For substrate relationships, thin grey lines = infaunal siphonate, black dotted lines = infaunal asiphonate, black dashed lines = epifaunal, light grey thick lines = boring. For feeding mode, thin grey lines = suspension feeder, light grey thick lines = carnivore, black dotted lines = chemosymbiont, black dashed lines = deposit feeder. Mosaic plots (on the right)

Environmental parameters such as temperature and resource availability have been mechanistically linked to intra-specific size–latitude trends (Lonsdale & Levinton, 1985; Cardoso & Defeo, 2003; Arendt, 2011). SST and latitude are themselves strongly correlated, and factors correlated with latitude will tend to correlate with temperature, even in the absence of direct causal links. However, we find no consistent evidence for their role in shaping family-level size patterns. Although it is true that mean annual SST, the annual range of SST and mean annual NPP are correlated with body size for some families on some coastlines, even within a family these patterns are spatially inconsistent – it is rare for a given environmental parameter to be the most significant predictor in even two out of four coastlines for a single family. While it is possible that body size evolution within a family has been influenced by temperature and resource availability differently in different regions, it is clear that environmental variables play no consistent global role in influencing size–latitude patterns for bivalve families in general. Inter-specific patterns are emergent properties of species assemblages influenced by complex evolutionary and ecological trade-offs involving not only growth rates and resource acquisition but also predation risk, reproductive potential and lifespan (especially in species with indeterminate growth). Thus, our failure to find consistent correlations with temperature and productivity does not preclude their potential importance in shaping intra-specific size–latitude trends. It is possible that body size is mechanistically related to temperature and/or productivity only for species in those families which show significant correlations (Fig. 3). Alternatively, it may be that correlations between size and temperature/productivity are generally intra-specific phenomena, and that body size patterns within families are influenced by numerous other factors that obscure the environmental correlations. Our data cannot distinguish between these possibilities.

It is notable that size trends are substantially more common in the West Pacific compared with other coastlines. The West Pacific is a well-known global diversity hotspot for bivalves (as for numerous other taxa). We find little evidence that size–latitude trends are related to diversity *per se* – the most species-rich families are no more or less likely to exhibit patterns than species-poor families – but the geographic pattern does suggest that historical contingency may play a critical role in establish-

ing size trends, even if it does not influence their direction. Historical events in particular regions may have selected for body size differently in different lineages and/or functional groups, contributing to present-day size patterns with no simple link to current environmental factors.

CONCLUSIONS

This study shows, for the first time, enormous diversity in size–latitude relationships for a large group of marine invertebrates. Variability in size–latitude patterns may well be the rule for ectotherms (Lindsey, 1966; Ashton & Feldman, 2003; Chown & Gaston, 2010), although more global-scale inter-specific studies are needed. This study suggests that size–latitude trends may be more spatially variable than previously appreciated, at least in the oceans. Many bivalve families show strong trends in only one hemisphere or on only one coastline, clearly indicating that regional patterns may not be mirrored in the opposite hemisphere and may not extend to the entire globe (Figs 2 & 3, Fig. S1 in Appendix S1). This variation among regions is striking, and suggests that macroecological patterns are driven by diverse processes (past or present) in different regions and for different lineages. Macroecological studies of regional datasets should thus consider the possibility that unsampled regions might show contradictory patterns, and that enlarging the study area or taxonomic coverage could yield insights that differ from a more narrowly focused analysis.

Latitudinal trends in body size are probably related to latitudinal trends in speciation and extinction rates. Size is phylogenetically conserved in bivalves, while origination and extinction show strong latitudinal variation (Jablonski *et al.*, 2006). Furthermore, palaeontological data show that extinctions are size-selective in some lineages (Smith & Roy, 2006), sometimes show different phylogenetic signals in different regions (e.g. at the two poles, Krug *et al.*, 2010) and generally show strong phylogenetic conservatism at higher taxonomic levels (Roy *et al.*, 2009). Geographic range shifts may also be size-selective in modern and fossil bivalves (Roy *et al.*, 2001). Thus, fully understanding size–latitude relationships may require a detailed understanding of the extinction, origination and invasion history for a region/lineage and they cannot be viewed solely as the equilibrium by-products of physiological responses to temperature or

Figure 5 Continued

indicate the proportion of different size–latitude trends for the functional group/coastline combinations shown on the left. The width of each mosaic column indicates the proportion of families falling into that functional group for the coastline indicated. The height of each mosaic box shows the relative proportion of each kind of trend: Bergmann trends (white), converse Bergmann trends (dark grey), or mixed trends (continually increasing or decreasing across the equator, light grey). Mobility classes: I = immobile, M = mobile, MM = mixed mobility. Substrate relationships: B = boring, E = epifaunal, IA = infaunal asiphonate, IS = infaunal siphonate, N = nestling, SI = semi-infaunal, SM = mixed substrate relationships. Feeding modes: C = carnivore, Ch = chemosymbiont, D = deposit feeding, S = suspension feeding. Dashed lines indicate that no significant patterns are exhibited for that functional group on the coastline shown – for example, no immobile families exhibited Bergmann trends in the West Atlantic, as indicated by the dashed line in the first cell of the topmost mosaic plot. Mosaic plots for all functional axes on all coastlines are shown in Fig. S3 in Appendix S1. WAtl = West Atlantic; WPac = West Pacific; EPac = East Pacific.

resource availability. For marine bivalves, which have a rich fossil record, hypotheses that present-day patterns result from spatially heterogeneous extinction, origination and range shifts could be tested by examining size trends in time slices that have not recently been subjected to an extinction pulse and repeated biogeographic upheavals related to glacial cycles. Future research should continue to evaluate how evolutionary, ecological and biogeographic dynamics interact to shape modern macroecological patterns.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supporting figures and tables.

Appendix S2 Regression results.

BIOSKETCH

Sarah K. Berke is interested in functional, behavioural, ecological and taxonomic diversity at a variety of scales.

Our research group is broadly interested in the evolutionary, ecological, and biogeographic dynamics underlying the earth's major diversity patterns. S.K.B. and D.J. together conceived of the study. S.K.B. collected most body size data (with assistance from D.J., A.K. and A.T.), conducted all analyses, and wrote the text. All authors contributed intellectually to analytical issues and data interpretation, and all commented on the text. D.J., A.K., S.K.B. and A.T. contribute to and maintain the world bivalve database.

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