

Latitudinal distribution of body size in north-eastern Pacific marine bivalves

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Abstract

Aim To understand the latitudinal patterns in body size distributions of north-eastern Pacific bivalves, as well as the factors influencing those patterns.

Locations The north-eastern Pacific continental shelf from 5 °S latitude to 70 °N latitude.

Methods We used data on the body size and latitudinal ranges of 915 species of north-eastern Pacific marine bivalves to test for the presence of interspecific latitudinal size trends. We tested for trends in both mean body size as well as variance in body size using randomization tests.

Results Overall, there is no significant linear relationship between either mean size or variance in size and latitude. Rather, there is a mid-latitude trough and peak in mean body size and variance in body size, respectively, with changes in the sign of the correlations occurring at provincial boundaries. A significant decreasing trend in mean size with latitude exists within the tropical Panamic province. In contrast, variance in body size shows a significant increasing trend with latitude within the tropics, and a significant decreasing trend with latitude in the cold temperate and Arctic provinces. For north-eastern Pacific bivalves, latitudinal trends in mean body size and variance in body size show very little correlation with latitudinal trends in species richness. Close to an order of magnitude difference in species numbers between tropical and polar latitudes does not appear to significantly affect either mean size or variance in size. Changes in mean body size associated with biogeographic boundaries are significantly larger than changes elsewhere along the range.

Main conclusions The spatial distribution of major environmental barriers along the north-eastern Pacific margin plays a major role in structuring the latitudinal distribution of body size in marine bivalves along this coast.

Keywords

Body size, latitude, bivalves, diversity, biogeography.

INTRODUCTION

Body size correlates strongly with many physiological, ecological and life-history traits, and is considered to be one of the most important attributes of organisms (McMahon & Bonner, 1983; Peters, 1983; McKinney, 1990; Blackburn & Gaston, 1994; West *et al.*, 1997). In addition, body size can have an important influence on the organization of

ecological communities (Lawton, 1990). Thus considerable attention and debate has been focused on the spatial distribution of body size, especially across large environmental gradients such as those associated with latitude (Cushman *et al.*, 1993; Blackburn & Gaston, 1996). Several hypotheses have been proposed that posit a relationship between latitude and body size. Of these, the best known trend in body size is Bergmann's rule, which states that body size increases with increasing latitude (Bergmann, 1947). Bergmann's rule has been tested for both endotherms and ectotherms, and at different taxonomic levels, but considerable debate exists about the generality of the pattern as well as about the

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underlying processes driving the pattern (e.g. James, 1970; McNab, 1971; Geist, 1987; Blackburn & Gaston, 1996; Mousseau, 1997; Partridge & Coyne, 1997).

One hypothesis relating body size and latitude is based on latitudinal changes in energy availability (i.e. the species-energy hypothesis, see Wright *et al.*, 1993). This hypothesis predicts smaller body size at high latitudes where energy availability is reduced relative to equatorial regions (Turner & Lennon, 1989; Cushman *et al.*, 1993). Energy requirements of species have also been used to link spatial patterns of species richness and body size; the positive scaling of energy requirements with size should translate into an inverse relationship between species richness and body size (Cousins, 1989; Blackburn & Gaston, 1996). Thus for groups that show a strong latitudinal gradient in species richness, this hypothesis predicts that body size should increase with latitude in accordance with Bergmann's rule.

The mechanisms that have been proposed to explain latitudinal size trends largely focus on physiological and ecological aspects. Biogeographic and evolutionary dynamics have received much less attention in this context. Yet given the relationships between species range size and body size (see Brown, 1995; Brown & Nicoletto, 1998), biogeography should play an important role in shaping latitudinal size trends. In particular, the factors that control the latitudinal distribution of species' geographical ranges may also play a role in shaping the latitudinal distribution of body size.

Predictions about latitudinal trends in body size have been tested primarily in vertebrates, with relatively little work focusing on the latitudinal distribution of body size for invertebrates (May, 1978; Barlow, 1994; Hawkins & Lawton, 1995). For some marine invertebrate groups, variations in size with depth have been quantified (Rex & Etter, 1998; Rex *et al.*, 1999) but very little is known about latitudinal trends in body size. In this study, we quantify the latitudinal distribution of body size in north-eastern Pacific marine bivalves, from the equator to northern Alaska, and explore some of the processes that may structure latitudinal size trends. We use a randomization approach to test for significant relationships between body size and latitude both across the entire range of the study as well as within biogeographical provinces. The results show that for these bivalves, neither Bergmann's rule nor species-energy hypothesis can explain the latitudinal patterns in body size. Hence we use resampling techniques and nonparametric statistics to determine whether the observed latitudinal patterns in body size could be driven by (1) the strong latitudinal gradient in species richness that characterizes north-eastern Pacific bivalves, (2) phylogenetic effects, or (3) environmental changes associated with major biogeographical barriers. We focus on north-eastern Pacific marine bivalves in the northern hemisphere because their diversity and latitudinal distributions are very well known (Roy *et al.*, 1994). This study consists of 915 species, covers over 70° of latitude and is the most extensive analysis of its kind ever undertaken for marine invertebrates.

METHODS

Data

We compiled the latitudinal ranges and body sizes of 915 species of bivalves living on the north-eastern Pacific shelf (depths shallower than 200 m), from the equator to the Arctic Ocean (70 °N). Data on the latitudinal distribution of bivalve species were obtained from an existing data base of north-eastern Pacific mollusks (Jablonski & Valentine, 1990; Roy *et al.*, 1994). Body size data were compiled through an exhaustive search of the primary literature and from major museum collections. Previous studies of latitudinal distribution of body size have used a number of different measures, ranging from linear morphological dimensions (such as length) to estimates of body mass (Blackburn & Gaston, 1994). In this study, we use the geometric mean of length and height of the bivalve shell as a measure of size. This simple metric has been used by a number of previous workers and attempts to partially standardize for interspecific shape differences (Stanley, 1986; Jablonski, 1996; Jackson *et al.*, 1996). Each species is represented in our analyses by its maximum reported size, rounded off to the nearest millimetre. Blackburn & Gaston (1998) have recently pointed out that macroecological studies often fail to include all species in an assemblage and that such sampling bias can potentially have an effect on the observed patterns. In this study we have attempted to reduce such bias by including nearly all species of bivalves described from the north-eastern Pacific shelf. Thus, the patterns documented here represent the current state of knowledge about the north-eastern Pacific bivalve fauna.

Statistical analyses

To investigate the relationship between body size and latitude, we divided the north-eastern Pacific shelf into 2° latitudinal bins and calculated both the mean and variance in body size for all species occurring within each bin. All analyses were carried out using log transformed size data. We then tested for latitudinal trends in both mean body size and variance in body size. Mean body size provides a representation of the species pool within each latitudinal band and is the metric most commonly used to study interspecific latitudinal patterns in body size (e.g. Cushman *et al.*, 1993; Hawkins & Lawton, 1995). However, variance in body size may also be informative from an ecological perspective. For continuous morphological characters such as size, variance is a useful measure of the dispersion among forms and can be considered as a measure of morphological disparity (Roy & Foote, 1997; see also Ricklefs & Miles, 1994).

The relationship between body size and latitude is difficult to test using parametric regression because of the spatial autocorrelation present in the data; as individual species occur in multiple latitudinal bins the data points are not independent. Past studies have dealt with the problem of spatial autocorrelation by foregoing statistical analysis of the

data (e.g. Hawkins & Lawton, 1995), by acknowledging the problem but using parametric regression nonetheless (Barlow, 1994), or by using the midpoint method that counts each species only once at the midpoint of its latitudinal range (Hawkins & Lawton, 1995). The midpoint method does produce independent data points, but it assumes that species range end points are distributed evenly in space rather than being clustered at biogeographic boundaries. This assumption is violated in our data where species range end points tend to be clustered at provincial boundaries (Roy *et al.*, 1994). Thus, in our case the midpoint method inflates the species richness in latitudes near the centre of a province and can produce an artifactual pattern. A second, and perhaps a more important argument against using the midpoint method is that the spatial autocorrelation present in the data is biologically meaningful, and should be taken into account when evaluating the relationship between size and latitude (Cushman *et al.*, 1993). Thus in this study we have chosen to use randomization tests to evaluate the significance of trends in our data. All randomizations were performed using Matlab (the Mathworks, Natick, MA, USA) and the program is available from the authors.

The effect of latitude on body size

We computed the slope of the relationship between latitude and mean body size as well as variance in body size for each 2° latitudinal bin using least squares regression. The size data were all log transformed. We computed the slopes for the entire data as well as for the tropical species (0–23 °N), and the cold temperate to polar species (36–70 °N; see below) separately. We tested the significance of the least-squares slope using a randomization procedure similar to that used by Cushman *et al.* (1993). First we generated a vector, each element of which was the range of a single species. We then randomly assigned a body size (chosen without replacement from the observed pool of species sizes) to each range and calculated the mean body size and variance in body size within each 2° latitudinal bin. Thus, both the latitudinal diversity gradient and the spatial autocorrelation present within the original data set was preserved, but body size was randomized with respect to range (and therefore latitude). We used the estimates of mean body size and variance in body size resulting from the randomization to generate regression coefficients of both mean body size and variance in body size on latitude. We repeated the randomization 100 times (500 times for variance estimates) and the *P*-value for the test is the proportion of randomized slopes that exceeded the slopes of the observed regressions (see Manly, 1991; Cushman *et al.*, 1993). Thus, we tested the null hypothesis that body size is random with respect to latitude given a latitudinal gradient in diversity. When testing the significance of the regressions for the tropical species, we sampled only from the body sizes of species within the Panamic province. Likewise, we only used body sizes from species occurring in the cold temperate and polar regions when testing the significance of the regression slopes within that region.

The effect of species richness on body size–latitude relationships

As north-eastern Pacific bivalves show a strong latitudinal diversity gradient (Fig. 1), we used resampling to determine whether any observed latitudinal trend in mean size is because of diversity changes along latitude. We sampled randomly, without replacement, an equal number of species from each latitudinal bin where the number of species sampled from each bin was equal to the number of species present in the least diverse bin within that province. We computed the mean body size within each bin for the resampled data and calculated the regression coefficients of mean body size on latitude. The procedure was repeated 1000 times and the *P*-value of the test was again the proportion of resampled slopes that were greater than the observed slope. The resamplings were carried out separately for the tropical species pool and the cold temperate to polar species pools. The null model here is that the latitudinal trend in body size is independent of species richness.

Effects of phylogeny

While phylogenetic effects have been shown in some cases to influence geographical trends in body size (Taylor & Gotelli, 1994), direct analysis of the influence of phylogeny requires a well resolved cladogram (Felsenstein, 1985; Harvey & Pagel, 1991). Unfortunately no such phylogeny is currently available for the 915 species of bivalves included in this study or even for any single large north-eastern Pacific bivalve family. Thus we tested for phylogenetic effects indirectly by comparing the latitudinal patterns of body size we observed at the species-level to those observed within individual clades as well as at the family level. For the family level analyses, we used the median size for that family as a representative measure of body size within the family. We then calculated the mean and variance in body size of all families present within each 2° latitudinal bin and used the randomization test outlined above to determine the significance of latitudinal trends in body size at the family level. Finally, we also quantified latitudinal size trends within individual families by separately analysing the three most species-rich families of north-eastern Pacific bivalves, Veneridae, Mytilidae, and Tellinidae.

Effects of biogeography

Along the north-eastern Pacific margin, biogeographic boundaries represent contacts between major water masses or water types, and hence represent significant environmental barriers that are characterized by the clustering of species range end points (Valentine, 1966; Roy *et al.*, 1994). These boundaries have been shown to exert an important control on the shape of the latitudinal gradient in species richness (Roy *et al.*, 1994, 1998). To determine if these biogeographic boundaries also influence latitudinal size trends, we computed the amount by which mean body size differs between adjacent 2° latitudinal bins. We then compared the differences between adjacent bins that straddle provincial boundaries with the differences between adjacent bins within a single province using a Mann–Whitney *U*-test.

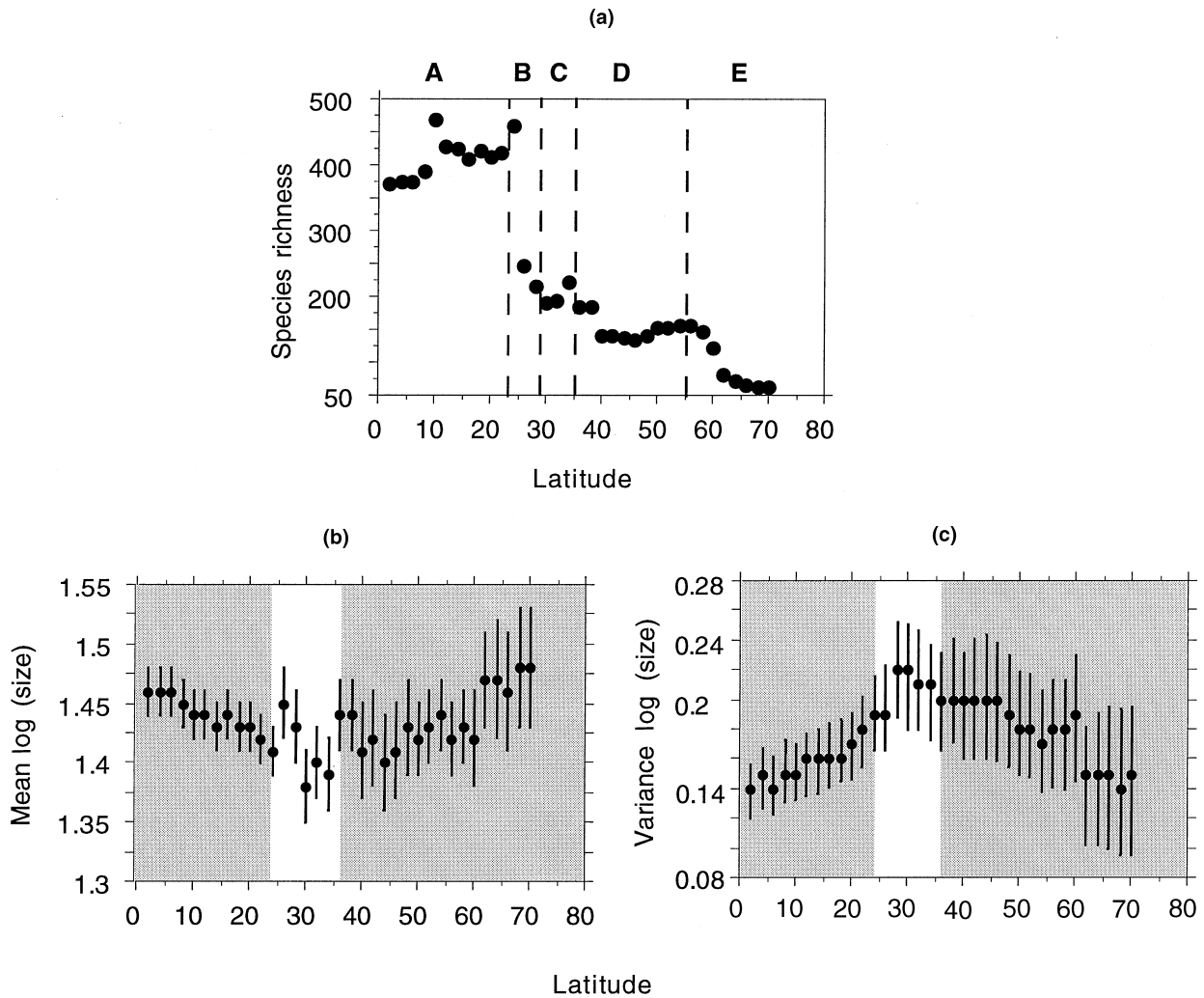


Figure 1 (a) Latitudinal trend in diversity for north-eastern Pacific bivalves. Species diversity is highest near the equator and declines toward the pole. The dashed vertical lines mark the boundaries between major biogeographic provinces: (A) Panamic province, (B) Surian province, (C) Californian province, (D) Oregonian province, and (E) Arctic province. The lower panels show the latitudinal trends in (b) mean and (c) variance of body size for north-eastern Pacific bivalves. Error bars for the mean are ± 1 SE and those for variances represent the bootstrapped 95% confidence intervals. Latitudinal trends were examined separately for the Panamic province (shaded region to the left of the graphs) and the combined Oregonian and Arctic provinces (shaded region to the right of the graphs).

RESULTS

For our data set as a whole, there is no significant linear relationship between mean body size and latitude (Fig. 1, Table 1). In fact, mean body size for our lowest and highest latitude assemblages is surprisingly similar. Mean size tends to decrease with latitude within the Panamic province, reaches its lowest value in the warm temperate Californian province, and increases with latitude in the Oregonian and Arctic provinces (latitude $> 34.5^\circ\text{N}$; Fig. 1). Randomization tests show that the decreasing trend in mean size with latitude within the Panamic province is significant (Table 1) but the apparent increase in mean size with latitude within the Oregonian and Arctic provinces is not (Table 1). North-eastern Pacific bivalves show a strong latitudinal gradient in

species richness with the tropical Panamic province (5°S – 23°N) harbouring the largest number of species and a rapid decrease in species richness outside the tropics (Roy *et al.*, 1994; Fig. 1). The diversity trend shows a stepwise pattern with the major declines in diversity being concentrated at the provincial boundaries (Valentine, 1966; Roy *et al.*, 1994, 1996). Resampling analyses reveal no significant effects of species richness on latitudinal trends in mean size (for the Panamic province $P = 0.24$ based on 1000 iterations; for the Oregonian and Arctic provinces $P = 0.28$).

Latitudinal trends in variance (or disparity) in body size in north-eastern Pacific bivalves differ from latitudinal trends in mean size. Lowest variance in body size is seen in tropical as well as arctic assemblages while maximum variance in body size is present in mid-latitude or warm temperate faunas

Table 1 Estimates of the regression slope of mean body size on latitude within the Panamic (tropical) province, the combined Oregonian and Arctic provinces, and across all latitudes (5 °S–70 °N) at both the species and family levels. The statistical significance of the regression slopes were tested using both a parametric approach and the resampling technique described in the text. Because the resampling technique is more conservative, it was only used for those regressions which were found to be statistically significant using the parametric approach

| | Slope | P-value | |
|------------------|----------|------------|-----------|
| | | Parametric | Resampled |
| Species-level | | | |
| All latitudes | 0.000136 | 0.51 | — |
| Tropical | −0.0023 | < 0.0001 | 0 |
| Oregonian–Arctic | 0.0020 | 0.0002 | 0.13 |
| Family level | | | |
| All latitudes | 0.0009 | 0.015 | 0.196 |
| Tropical | −0.0031 | 0.006 | 0.03 |
| Oregonian–Arctic | 0.0043 | < 0.0001 | 0.01 |

Table 2 Estimates of the regression slope of variance in body size on latitude within the Panamic (tropical) province, the combined Oregonian and Arctic provinces, and across all latitudes (5 °S–70 °N) at both the species and family levels. The statistical significance of the regression slopes were tested using both a parametric approach and the resampling technique described in the text. Because the resampling technique is more conservative, it was only used for those regressions which were found to be statistically significant using the parametric approach

| | Slope | P-value | |
|------------------|---------|------------|-----------|
| | | Parametric | Resampled |
| Species-level | | | |
| All latitudes | 0.00013 | 0.50 | — |
| Tropical | 0.0020 | < 0.0001 | 0 |
| Oregonian–Arctic | −0.0021 | < 0.0001 | 0.04 |
| Family level | | | |
| All latitudes | −0.0016 | < 0.0001 | 0.004 |
| Tropical | 0.0013 | 0.003 | 0.086 |
| Oregonian–Arctic | −0.0025 | < 0.0001 | 0.02 |

(Fig. 1). Thus, the latitudinal pattern for variance in body size is exactly opposite to that seen for mean body size. There is no significant linear relationship between latitude and variance in size across the entire range of the study (Table 2). However, variance in size shows a significant increasing trend with latitude within the Panamic province and a significant decreasing trend within the Oregonian and Arctic provinces (Table 2). The differences in the latitudinal patterns in variance vs. mean body size reflect changing shapes of the size frequency distributions (Fig. 2). Finally, changes in mean body size associated with biogeographic boundaries are significantly larger than changes elsewhere (Mann–Whitney *U*-test; $P = 0.0006$; Figs 1 & 4) indicating that provincial boundaries have a strong influence on latitudinal size trends.

As with the species level analysis, the family level data show no significant linear trend in mean body size when all provinces are combined (Table 1). However, the familial data do show a significant decrease in size with latitude within the Panamic province, a pattern again consistent with that seen at the species level (Table 1). Within the Oregonian and Arctic provinces we found a significant positive relationship between size and latitude for the familial data. This result is in the same direction as the species level pattern where the trend is not statistically significant (Table 1). We also found a significant overall negative relationship between variance in size and latitude at the family level, while at the species level there is no significant relationship. The within province trends in size variance for families are consistent with those seen at the species level (Table 2). The individual families of bivalves we examined show no consistent relationship between size and latitude, despite the fact that all three show strong latitudinal diversity gradients (Fig. 3). Mean size of species in both Veneridae and Mytilidae tend to decrease with latitude while species belonging to Tellinidae show the opposite pattern (Fig. 3).

DISCUSSION

Patterns of body size variation along latitude

Our results show that overall there is no latitudinal gradient in mean body size in north-eastern Pacific bivalves despite the presence of a strong latitudinal gradient in diversity. However, a significant negative relationship between mean size and latitude holds within the tropics, both at the species and family levels. Similarly, while we found no evidence for a general latitudinal trend in disparity in body size in these bivalves, significant relationships between latitude and disparity in size are present on a more regional scale, again at the species and family levels. Finally, the warm temperate assemblages appear anomalous in terms of body size as they exhibit the highest disparity and lowest mean size. Thus for the north-eastern Pacific bivalves, the relationship between latitude and size strongly depends on the spatial scale of observation as well as on the focal region; latitudinal size trends are present within some biogeographic provinces but are not significant when data from all provinces are combined. These results are consistent with previous studies which have shown that shapes of size frequency distributions change with spatial scales of observation. For example, frequency distributions of mammalian body sizes at the level of biomes were found to be intermediate between those seen at the local and continental levels (Brown & Nicoletto, 1991; Brown, 1995).

Although latitudinal trends in body size have long been of interest to biologists, surprisingly few studies have investigated interspecific latitudinal size trends in invertebrates over large spatial scales. Cushman *et al.* (1993) found an increase in body size with latitude for two subfamilies of ants in Britain and Northern Europe (between *c.* 50 and 70 °N), while bees in North America (between 25 and 50 °N) do not

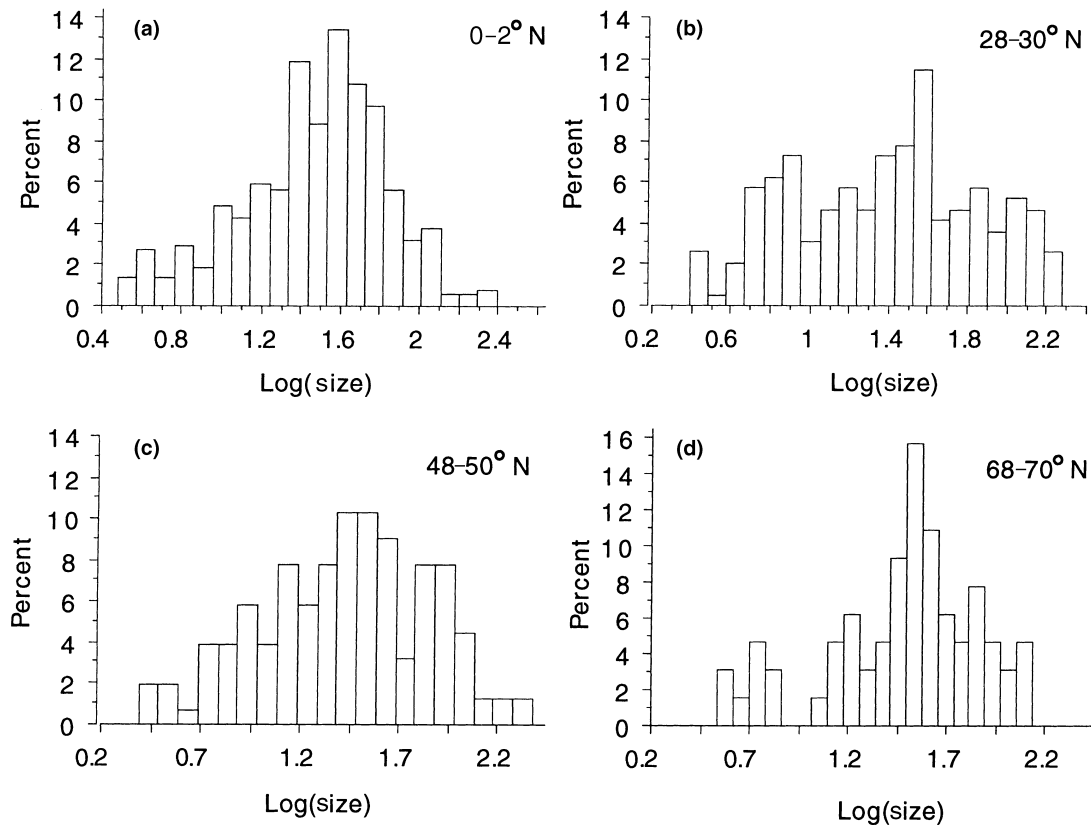


Figure 2 Size frequency distributions from representative 2° latitudinal bins from each of the (a) Panamic, (b) Californian, (c) Oregonian and (d) Arctic provinces.

show any significant relationship between size and latitude (Hawkins, 1995). Butterfly data from North America and Europe suggest that in extratropical regions size either does not change with latitude or increases slightly with latitude (Miller, 1991; Hawkins & Lawton, 1995). However, data for butterflies from the southern hemisphere tropics show a negative relationship between size and latitude (Barlow, 1994; Hawkins & Lawton, 1995). Interestingly enough, the North American and Australian butterfly data presented by Hawkins & Lawton (1995) seems to suggest that the trend may change in direction for butterflies at around 30 °N and 30 °S latitudes, respectively, perhaps in accordance with the trend reversal we found for bivalves between the tropical and cold temperate regions. Unfortunately, the available butterfly data are not sufficient to conclusively demonstrate such a reversal (see Hawkins & Lawton, 1995). Two other studies of interspecific insect size gradients are of limited use in the present context as they only provide tropical–temperate comparisons rather than latitudinal gradients. Nonetheless, these studies suggest that colony size in tropical ants is significantly smaller than those in temperate areas (Kaspari & Vargo, 1995) while body size of tropical insects tend to be larger than their temperate counterparts (Schoener & Janzen, 1968). None of the existing studies have

investigated latitudinal trends in disparity in body size (although see Schoener & Janzen, 1968).

For ectotherms in general, the available data suggest that there may not be any consistent relationships between body size and latitude, a situation similar to that in endotherms (see McNab, 1971; Cushman *et al.*, 1993). On a regional scale, the latitudinal size trend seen in butterflies from the southern hemisphere tropics (Barlow, 1994; Hawkins & Lawton, 1995) are very similar to those seen in tropical north-eastern Pacific bivalves. Based on only two studies it is premature to say whether such a negative relationship between size and latitude is a general rule for tropical invertebrate species assemblages; clearly data from other groups are needed. However, we do note that at the population level a negative relationship between size and latitude apparently is common for many insect species (Mousseau, 1997).

Size and latitude in marine bivalves

While the quantification of interspecific latitudinal patterns in body size is important for many ecological reasons, the processes that may underlie such patterns remain poorly understood (May, 1978; Lawton, 1991; Barlow, 1994;

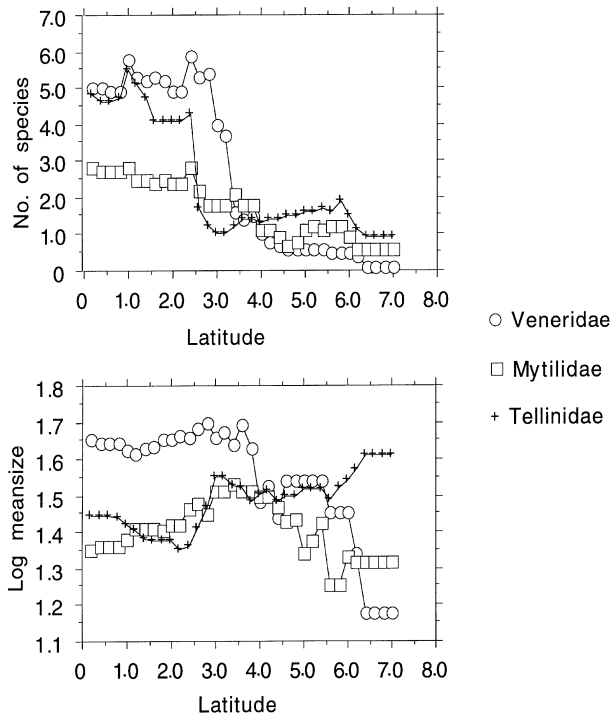


Figure 3 Latitudinal trends in species diversity and mean body size for the Veneridae, Mytilidae, and Tellinidae, the three largest families of northeastern Pacific bivalves. The assemblage level pattern of body size is not reflected in the latitudinal patterns of any of these three families, indicating that the overall pattern is not being driven by a single large clade.

Hawkins & Lawton, 1995). Proposed mechanisms for latitudinal trends in size include the availability of energy, heat-conservation, historical effects, ability to migrate, resource tracking and starvation-resistance (see McNab, 1971; Cushman *et al.*, 1993). The energy availability hypothesis is essentially an extension of the species-energy hypothesis which proposes that latitudinal changes in the availability of solar energy may account for latitudinal trends in species diversity (Wright, 1983; Turner & Lennon, 1989; Wright *et al.*, 1993; Fraser & Currie, 1996). For our data this hypothesis is important because it has been shown that patterns of energy availability are good predictors of latitudinal trends in species richness of north-eastern Pacific shallow marine mollusks (Roy *et al.*, 1998). However, on the equator to pole transect, the results presented here provide little support for the idea that energy availability strongly influences body size patterns in north-eastern Pacific bivalves. There is neither a significant negative relationship between size and latitude (Turner & Lennon, 1989) nor an inverse relationship between species richness and body size (Cousins, 1989). However, within the tropical Panamic province, we do find a significant negative relationship between size and latitude. Thus if energy availability is somehow an important determining factor for latitudinal size trends for north-eastern Pacific bivalves, its effect is felt only in the tropical areas.

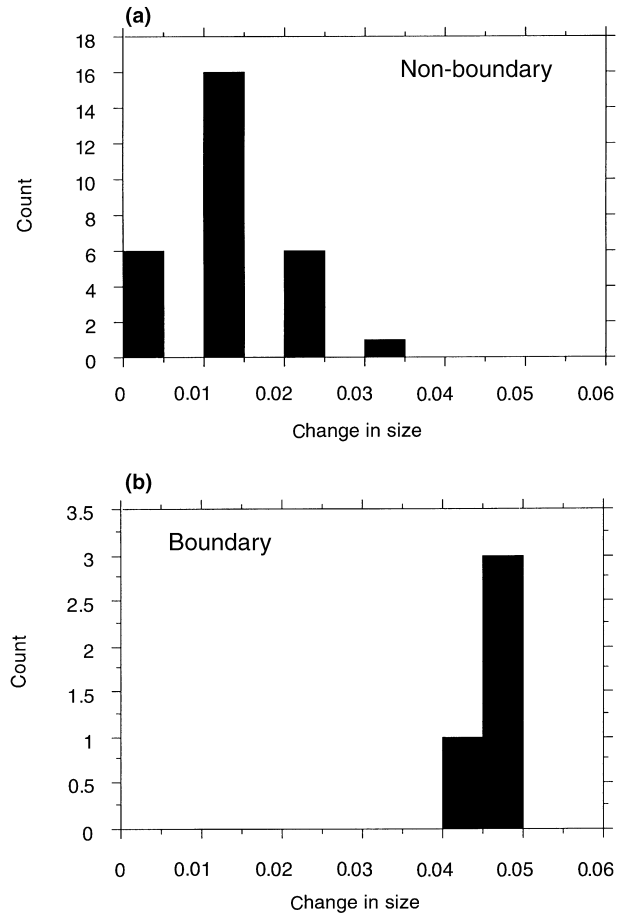


Figure 4 Size change between adjacent 2° latitudinal bands. (a) All bands that fall within a province and (b) bands that mark the biogeographic boundaries. The distributions are significantly different (Mann-Whitney *U*-test; $P = 0.0006$).

Biogeography and history, on the other hand, appear to be important in determining the latitudinal distribution of bivalve body size. Environmental barriers that exert a strong influence on the geographical ranges of north-eastern Pacific mollusks also play an important role in structuring the overall latitudinal trend in body size. In addition, the size-latitude relationship of north-eastern Pacific bivalves differs from province to province. This suggests that processes that influence within province size trends are different from those that determine large scale latitudinal trends in size. The latter would undoubtedly include historical processes such as speciation, extinction and biotic interchange (Ricklefs & Schluter, 1993). The consistency between the species level trends and family level trends in our data also supports an important role of history in shaping these patterns. However, the evolutionary dynamics underlying latitudinal trends in body size are poorly understood at present. In particular, the relationship between body size and species survivorship is a matter of debate. Size appears not to be important during mass extinctions but may turn out to be

important during background times, at least in certain groups (Pimm *et al.*, 1988; Pimm, 1991; Lawton, 1994; Gaston & Blackburn, 1995; Jablonski & Raup, 1995; Jablonski, 1996). In fact, for north-eastern Pacific marine bivalves, size has been argued to have influenced species survivorship during the Neogene (Stanley, 1986, 1990; Roopnarine, 1996). In addition, for bivalves in general and north-eastern Pacific mollusks in particular, there is also growing evidence that taxonomic turnover rates may differ between tropical and extratropical areas (Flessa & Jablonski, 1996). All of this suggests that history may indeed prove to be an important component of the latitudinal distribution of body size (also see Taylor & Gotelli, 1994). Further tests of historical hypotheses are hindered by the lack of well supported phylogenies for north-eastern Pacific bivalve clades. There is a clear need of such phylogenies along with actual size data from the north-eastern Pacific fossil record.

Finally a number of palaeontological studies have shown that temporal trends in taxonomic diversity (measured as taxon richness) often do not match temporal trends in morphological diversity (quantified as the distribution of taxa in morphological space) (Foote, 1997; Roy & Foote, 1997). While there is some evidence to suggest that interesting spatial trends in morphological diversity also exist in present day communities, quantitative data on how morphological diversity changes along environmental gradients such as those present along latitudes is lacking for most living taxa (review in Foote, 1997; Roy & Foote, 1997). Latitudinal trends in mean body size and disparity in body size documented here show little correlation with latitudinal trends in taxonomic diversity. It is remarkable that close to an order of magnitude difference in species numbers between tropical and polar latitudinal bands does not appear to significantly affect either mean body size or the variance in size. Thus our results support the notion that metrics based on morphological parameters tend to present a very different picture of biodiversity patterns compared with those based on counts of species or higher taxa (Foote, 1997; Roy & Foote, 1997).

ACKNOWLEDGMENTS

We thank T. Case, D. Jablonski, T. Price, J.W. Valentine and two anonymous reviewers for discussions and/or comments. Partial financial support for this project was provided by a Hellman Faculty Fellowship to KR and by a National Science Foundation Pre-Doctoral Fellowship to KM.

REFERENCES

- Barlow, N.D. (1994) Size distributions of butterfly species and the effect of latitude on species size. *Oikos*, **71**, 326–332.
- Bergmann, C. (1947) Über die Verhältnisse der Wärmeökonomie der Tiere zu ihrer Größe. *Göttinger Studien*, **1**, 595–708.
- Blackburn, T.M. & Gaston, K.J. (1994) Animal body size distributions: patterns, mechanisms and implications. *Trends in Ecology and Evolution*, **9**, 471–474.
- Blackburn, T.M. & Gaston, K.J. (1996) Spatial patterns in the body sizes of bird species in the New World. *Oikos*, **77**, 436–446.
- Blackburn, T.M. & Gaston, K.J. (1998) Some methodological issues in macroecology. *American Naturalist*, **151**, 68–83.
- Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago.
- Brown, J.H. & Nicoletto, P.F. (1991) Spatial scaling of species composition: body masses of North American land mammals. *American Naturalist*, **138**, 1478–1512.
- Brown, J.H. & Nicoletto, P.F. (1998) *Biogeography*, 2nd edn. Sinauer Associates, Massachusetts.
- Cousins, S.H. (1989) Species richness and energy theory. *Nature*, **340**, 350–351.
- Cushman, J.H., Lawton, J.H. & Manly, B.F.J. (1993) Latitudinal patterns in European ant assemblages: variation in species richness and body size. *Oecologia*, **95**, 30–37.
- Felsenstein, J. (1985) Phylogenies and the comparative method. *American Naturalist*, **125**, 1–15.
- Flessa, K.W. & Jablonski, D. (1996) The geography of evolutionary turnover: a global analysis of extant bivalves. *Evolutionary paleobiology* (eds D. Jablonski, D.H. Erwin and J.H. Lipps), pp. 376–397. University of Chicago Press, Chicago.
- Foote, M. (1997) The evolution of morphological diversity. *Annual Review of Ecology & Systematics*, **28**, 129–152.
- Fraser, R.H. & Currie, D.J. (1996) The species-energy hypothesis in a system where historical factors are thought to prevail: coral reefs. *American Naturalist*, **148**, 138–159.
- Gaston, K.J. & Blackburn, T.M. (1995) Birds, body size and the threat of extinction. *Philosophical Transactions of the Royal Society of London B*, **347**, 205–212.
- Geist, V. (1987) Bergmann's Rule is invalid. *Canadian Journal of Zoology*, **65**, 1035–1038.
- Harvey, P.H. & Pagel, M.D. (1991) *The comparative method in evolutionary biology*. Oxford University Press, Oxford.
- Hawkins, B.A. (1995) Latitudinal body-size gradients for the bees of the eastern United States. *Ecological Entomology*, **20**, 195–198.
- Hawkins, B.A. & Lawton, J.H. (1995) Latitudinal gradients in butterfly body sizes: is there a general pattern? *Oecologia*, **102**, 31–36.
- Jablonski, D. (1996) Body size and macroevolution. *Evolutionary paleobiology* (eds D. Jablonski, D.H. Erwin and J.H. Lipps), pp. 256–289. University of Chicago Press, Chicago.
- Jablonski, D. & Raup, D.M. (1995) Selectivity of end-Cretaceous marine bivalve extinctions. *Science*, **268**, 389–391.
- Jablonski, D. & Valentine, J.W. (1990) From regional to total geographic ranges: testing the relationship in Recent bivalves. *Paleobiology*, **16**, 126–142.
- Jackson, J.B.C., Jung, P. & Fortunato, H. (1996) Paciphilia revisited: Transisthmian evolution of the *Strombina* group. *Evolution and environment in tropical America* (ed by J.B.C. Jackson, A.F. Budd and A.G. Coates), pp. 234–270. University of Chicago Press, Chicago.
- James, F.C. (1970) Geographic size variation in birds and its relationship to climate. *Ecology*, **51**, 365–390.
- Kaspari, M. & Vargo, E.L. (1995) Colony size as a buffer against seasonality: Bergmann's rule in social insects. *American Naturalist*, **145**, 610–632.

- Lawton, J.H. (1990) Species richness and population dynamics of animal assemblages: patterns in body size: abundance space. *Philosophical Transactions of the Royal Society of London B*, **330**, 283–291.
- Lawton, J.H. (1991) Species richness, population abundances, and body sizes in insect communities: tropical versus temperate comparisons. *Plant–animal interactions: evolutionary ecology in tropical and temperate regions* (eds P.W. Price, T.M. Lewinsohn, G.W. Fernandes and W.W. Benson), pp. 71–89. Wiley, New York.
- Lawton, J.H. (1994) Population dynamic principles. *Philosophical Transactions of the Royal Society of London B*, **344**, 61–68.
- Manly, B.F.J. (1991) *Randomization and Monte Carlo methods in biology*. Chapman & Hall, New York.
- May, R.M. (1978) The dynamics and diversity of insect faunas. *Diversity of insect faunas* (eds L.A. Mound and N. Waloff), pp. 188–204. Blackwell, Oxford.
- McKinney, M.L. (1990) Trends in body-size evolution. *Evolutionary trends* (ed. K.J. McNamara), pp. 75–118. University of Arizona Press, Tucson.
- McMahon, T.A. & Bonner, J.T. (1983) *On size and life*. W. H. Freeman, New York.
- McNab, B.K. (1971) On the ecological significance of Bergmann's rule. *Ecology*, **52**, 845–854.
- Miller, W.E. (1991) Body size in North American lepidoptera as related to geography. *Journal of Lepidopterists' Society*, **45**, 158–168.
- Mousseau, T.A. (1997) Ectotherms follow the converse to Bergmann's rule. *Evolution*, **51**, 630–632.
- Partridge, L. & Coyne, J.A. (1997) Bergmann's rule in ectotherms: is it adaptive? *Evolution*, **51**, 632–635.
- Peters, R.H. (1983) *The ecological implications of body size*. Cambridge University Press, Cambridge.
- Pimm, S.L. (1991) *The balance of nature?* University of Chicago Press, Chicago.
- Pimm, S.L., Jones, H.L. & Diamond, J. (1988) On the risk of extinction. *American Naturalist*, **132**, 757–785.
- Rex, M.A. & Etter, R.J. (1998) Bathymetric patterns of body size: implications for deep-sea biodiversity. *Deep-Sea Research II*, **45**, 103–127.
- Rex, M.A., Etter, R.J., Clain, A.J. & Hill, M.S. (1999) Bathymetric patterns of body size in deep-sea gastropods. *Evolution*, **53**, 1298–1301.
- Ricklefs, R.E. & Miles, D.B. (1994) Ecological and evolutionary inferences from morphology: an ecological perspective. *Ecological morphology* (eds P.C. Wainwright and S.M. Reilly), pp. 13–41. University of Chicago Press, Chicago.
- Ricklefs, R.E. & Schluter, D. (1993) Species diversity: regional and historical influences. *Species diversity in ecological communities* (eds R.E. Ricklefs and D. Schluter), pp. 350–363. University of Chicago Press, Chicago.
- Roopnarine, P.D. (1996) Systematics, biogeography and extinction of chionine bivalves (Bivalvia: Veneridae) in tropical America: early Oligocene-recent. *Malacologia*, **38**, 103–142.
- Roy, K. & Foote, M. (1997) Morphological approaches to measuring biodiversity. *Trends in Ecology and Evolution*, **12**, 277–281.
- Roy, K., Jablonski, D. & Valentine, J.W. (1994) Eastern Pacific Molluscan provinces and latitudinal diversity gradient: no evidence for 'Rapoport's Rule'. *Proceedings of the National Academy of Sciences, USA*, **91**, 8871–8874.
- Roy, K., Jablonski, D. & Valentine, J.W. (1996) Higher taxa in biodiversity studies: insights from Eastern Pacific marine mollusks. *Philosophical Transactions of the Royal Society of London B*, **351**, 1605–1613.
- Roy, K., Jablonski, D., Valentine, J.W. & Rosenberg, G. (1998) Marine latitudinal diversity gradients: tests of causal hypotheses. *Proceedings of the National Academy of Sciences, USA*, **95**, 3699–3702.
- Schoener, T.W. & Janzen, D.H. (1968) Notes on environmental determinants of tropical versus temperate insect size patterns. *American Naturalist*, **102**, 207–224.
- Stanley, S.M. (1986) Population size, extinction, and speciation: the fission effect in Neogene Bivalvia. *Paleobiology*, **12**, 89–110.
- Stanley, S.M. (1990) The general correlation between rate of speciation and rate of extinction: fortuitous causal linkages. *Causes of evolution: a paleontological perspective* (eds R.M. Ross and W.D. Allmon), pp. 103–127. University of Chicago Press, Chicago.
- Taylor, C.M. & Gotelli, N.J. (1994) The macroecology of *Cyprinella*: correlates of phylogeny, body size and geographical range. *American Naturalist*, **144**, 549–569.
- Turner, J.R.G. & Lennon, J.J. (1989) Species richness and the energy theory. *Nature*, **340**, 351.
- Valentine, J.W. (1966) Numerical analysis of marine molluscan ranges on the extra-tropical northeastern Pacific shelf. *Limnology and Oceanography*, **11**, 198–211.
- West, G.B., Brown, J.H. & Enquist, B.J. (1997) A general model for the origin of allometric scaling laws in biology. *Science*, **276**, 122–126.
- Wright, D.H. (1983) Species-energy theory: an extension of species-area theory. *Oikos*, **41**, 496–506.
- Wright, D.H., Currie, D.J. & Maurer, B.A. (1993) Energy supply and patterns of species richness on local and regional scales. *Species diversity in ecological communities* (eds R.E. Ricklefs and D. Schluter), pp. 66–74. University of Chicago Press, Chicago.

BIOSKETCHES

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