Eastern Pacific molluscan provinces and latitudinal diversity gradient: No evidence for "Rapoport's rule"

(biogeography/marine Mollusca/provincial structure)

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ABSTRACT "Rapoport's rule," which has gained wide acceptance as a potential explanation for latitudinal and other diversity gradients, holds that mean latitudinal range of species decreases toward the equator. We analyzed latitudinal ranges of 2838 eastern Pacific marine molluscan species, a subset of which figured in the original formulation of Rapoport's rule, and failed to find the predicted trends. Instead, species diversity gradients and range magnitudes appear to vary independently, with the spatial distribution of major oceanographic barriers exerting a strong influence on latitudinal ranges. Biogeographic structure should, therefore, be an important element in the assessment of diversity patterns.

Latitudinal diversity gradients characterize many marine and terrestrial biotas, and, although the factors that produce them have long been debated, they remain enigmatic, "the major, unexplained pattern in natural history" (R. E. Ricklefs in 1; see also ref. 2). Explanations of latitudinal gradients have invoked factors ranging from competition, predation, habitat patchiness, and habitat area to environmental stability and productivity (3, 4). A recent hypothesis that is gaining some acceptance relies upon "Rapoport's rule"—that there is a decrease in average latitudinal range toward lower latitudes (5, 6). It is argued that the latitudinal diversity gradient is generated by a narrowing of climatic tolerance among increasingly tropical organisms: not only could more species be packed into a given tropical region, but, with narrower ranges and dispersal abilities similar to species in higher latitudes, many tropical species will tend to spill over into adjacent habitats and thereby inflate regional diversity (5). The proposal of Rapoport's rule was supported by latitudinal range data for a variety of marine and terrestrial organisms (5, 6), and despite some authors' failure to detect the pattern (7–9), the rule has been widely accepted as codifying a common pattern in nature (10–12). It has been incorporated into texts and popular books on biodiversity as a preferred explanation for latitudinal diversity gradients (13–15) and has been extended to analyses of elevational, bathymetric, and other gradients (16, 17). It has even been the basis for predictions of the biotic consequences of global warming and other aspects of conservation biology (18, 19). In this report we analyze the latitudinal ranges of eastern Pacific marine mollusks, a subset of which figured in the original supporting data of Stevens (5, 6), to quantify the biogeographic structure of this fauna and thereby test the validity of Rapoport's rule.

We compiled latitudinal ranges for 2838 species of shelled gastropods and bivalves recorded living in water shallower than 200 m from Peru to the Arctic Ocean. The sources for molluscan ranges are listed in ref. 20, which were updated by an extensive search of the primary molluscan literature and some more recent compilations (e.g., refs. 21–23); ranges are

rounded to the nearest degree. The latitudinal diversity gradient was quantified by pooling all species whose ranges crossed a given 5° latitudinal band, thereby approximating regional diversity. In pooling species between 23° N and 32° N, we tallied species occurring in the Gulf of California separately from those that occur along the outer Baja California coast. This was necessary because two very different water masses exist at the same latitude there, separated by the peninsula of Baja California. Latitudes of the Aleutian arc and the corresponding mainland are also crossed twice (or three times) by shorelines; however, the Aleutians are largely east–west and the whole region is bathed by Pacific subarctic water. In testing for Rapoport's rule, we calculated mean, median, and modal ranges for species in each 5° band. Stevens (5) used the mean latitudinal range of all species that he sampled in a given latitudinal band to argue for decreasing ranges toward the tropics. Rohde *et al.* (7) pointed out that Stevens's method counted the same species multiple times and hence resulted in nonindependent samples; to circumvent this problem, they suggested calculating means only of species whose midpoints fall in a given latitudinal band (see also ref. 9). Although we calculated the means for our data using both methods, they are inappropriate measures of central tendency, given the strongly nonnormal distributions of species latitudinal ranges for any given latitudinal band; thus, we also calculated median and modal ranges to test for latitudinal gradients. In calculating means, both Stevens (5) and Rohde *et al.* (7) rounded the latitudinal ranges to the nearest 5°, but we have avoided such rounding.

Eastern Pacific marine mollusks exhibit a strong latitudinal diversity gradient from the equator to northern Alaska (Fig. 1A). Maximum diversity occurs between 5° N and 10° N, slightly north of the climatic equator near 5° N (26); greater sampling intensity in the Gulf of Panama relative to western Colombia and Ecuador may have affected the location of this peak. The diversity gradient has a stepped pattern, with major changes in diversity concentrated at provincial boundaries (Fig. 1A) (24).

Mean latitudinal ranges of the eastern Pacific marine mollusks do not exhibit the correlation with latitude predicted by Rapoport's rule for either of the protocols that we used. Means calculated using Stevens's method and plotted against latitude fail to show the expected trend of increasing mean ranges with increasing latitude (Fig. 1B); if anything, they decrease toward highest latitudes. Means calculated using Rohde's method (7) show a similar pattern (not figured) but with higher scatter. The median and modal ranges remain remarkably stable from tropical to temperate areas and decrease toward the highest latitudes (Table 1).

In the original formulation of Rapoport's rule, North American marine mollusks were cited as showing a pattern of decreasing latitudinal ranges toward the tropics (5). However, the molluscan pattern was obtained by calculating mean ranges of pooled Atlantic and Pacific species using a small and apparently nonrandom sample (251 eastern Pacific species vs.
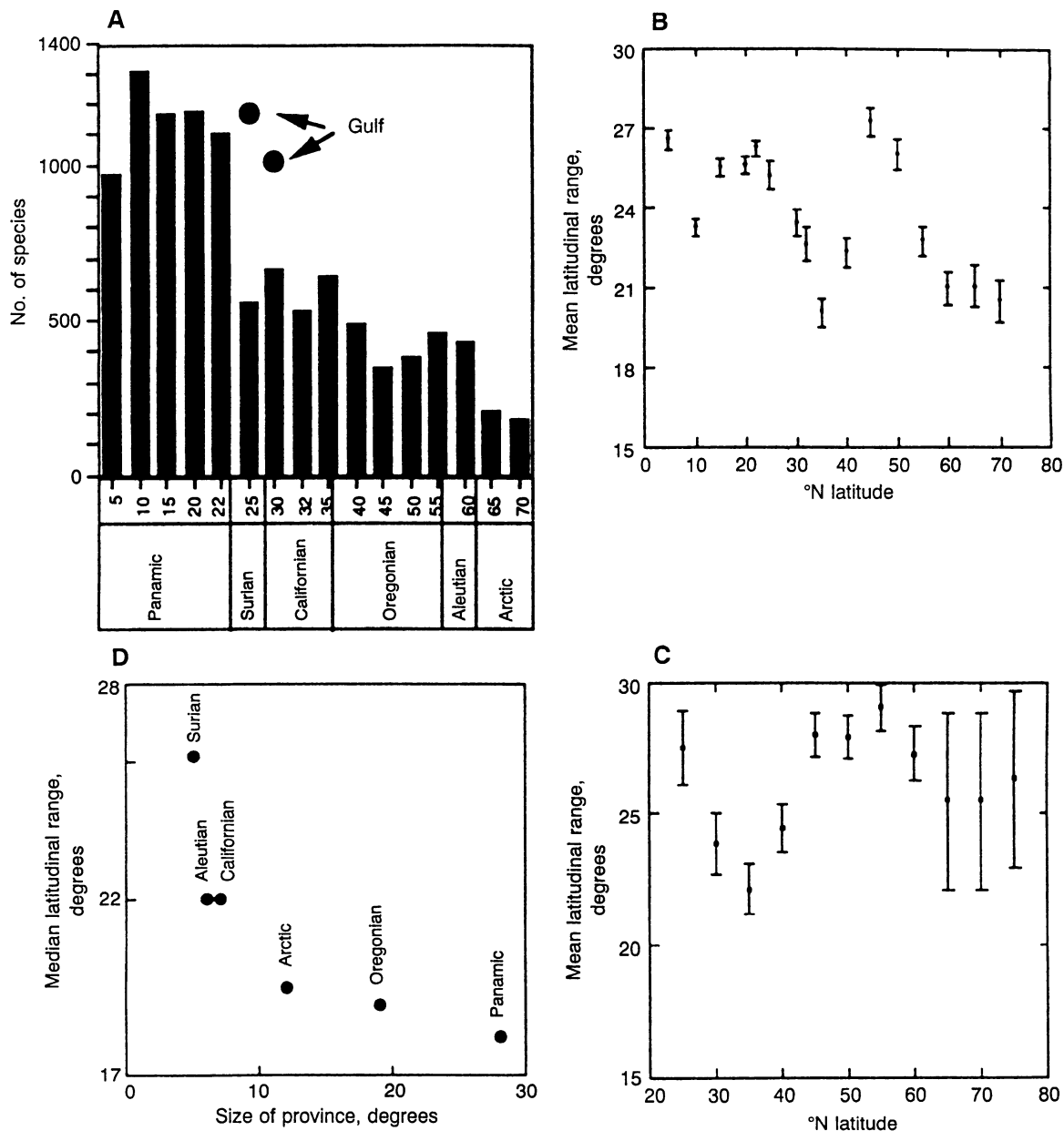
FIG. 1. Diversity patterns of eastern Pacific marine mollusks. (*A*) Regional diversity as a function of latitude. Each bar represents pooled data for a 5° band except between 22° N and 35° N, where the widths are adjusted to accommodate the Gulf of California. We have separated the Gulf species (solid circles) from those occurring along the outer coast of Baja (bars). The provinces are those defined in ref. 24; subsequent collecting in high latitudes has resulted in many range changes that bear upon our understanding of the biogeography of the low-diversity biotas there (see references in ref. 20); high-latitude provinces may thus require revision, but this does not affect the arguments or conclusions of this report. (*B*) Mean latitudinal ranges plotted against latitude; each point represents the mean range of all species occurring within a 5° band, with error bars of ±1 SEM. (*C*) Mean latitudinal ranges using the eastern Pacific species in Rehder (25), the data source for Stevens (figure 2 in ref. 5; figure 4.5 in ref. 6). As the geographic ranges in this guide tend to be very generalized, we used a coding scheme to transform them into latitudes (e.g., "southern Baja California" was coded as 23° N). The latitudinal range in the plot is that of Stevens; his data excludes almost all tropical species. (*D*) Median latitudinal ranges at the provincial scale; each point represents the median range of all species occurring in that province.

2838 species in our data base) that omitted virtually all species south of 25° N. We consider the problem of pooling species from two oceans to be particularly serious, given their very different biogeographic structures and different climatic and geologic histories. Hence we reanalyzed Stevens' data (25) in the proper biogeographic context (i.e., only eastern Pacific species) and failed to detect the predicted trend (Fig. 1*C*).

Rapoport's rule cannot be confirmed for eastern Pacific marine mollusks despite the presence of a striking latitudinal diversity gradient; in fact, lowest latitudinal ranges are associated with regions of lowest diversity, contrary to expectations. The molluscan pattern obtained by Stevens (5) appears to be an artifact arising from the combined effects of

poor sampling and pooling of data from two contrasting oceanographic situations (the western Atlantic and the eastern Pacific). In fact, Rohde *et al.* (7) pointed out that larger means for the high-latitude species could be an artifact resulting from the combined effect of small species numbers and the presence of a few long-ranging species. Given that the western Atlantic coast extends about 10° higher than the eastern Pacific coast and that Atlantic provinciality is not as strong, average species ranges in the Atlantic may be higher than those of the eastern Pacific, and the effect that Rohde *et al.* (7) note may apply there.

Although the primary controls on the latitudinal diversity gradient of eastern Pacific mollusks remain uncertain, the

Table 1.   Median and modal latitudinal ranges of eastern Pacific marine molluscan species as a function of latitude

Latitude, °N	Median range, degrees	Modal range, degrees
0–5	29	30–35
5–10	25	30–35
10–15	27	30–35
15–20	28	30–35
20–22	28	30–35
22–25	28	30–35
25–30	26	30–35
30–32	23	5–10
32–35	19	5–10
35–40	23	25–30
40–45	27	25–30
45–50	25	20–25
50–55	23	20–25
55–60	22	20–25
60–65	19	20–25
65–70	19	20–25

Calculations are based on ranges of all species occurring in a given latitudinal band.

distribution of range spans and the pattern of range endpoints appear to be related to the coastal oceanography of the region. Clusters of range endpoints have been used to define provincial boundaries, which are correlated with contacts between contrasting water masses or water types with distinctive temperature regimes (Fig. 2; refs. 24, 27–29). Since latitudes marked by provincial boundaries are thus more difficult to cross than intraprovincial latitudes, once species penetrate a province, their ranges may continue to the next water mass boundary. For example, the Panamic province has fully 35% of its species ranging from its northern boundary (at Cabo San Lucas, 23° N) to the equator. Similarly, in midlatitudes, the broad Oregonian province has 32% of its species ranging throughout the province, again suggesting that many species perceive the intraprovincial latitudes as physically homogeneous. However, broad provinces also
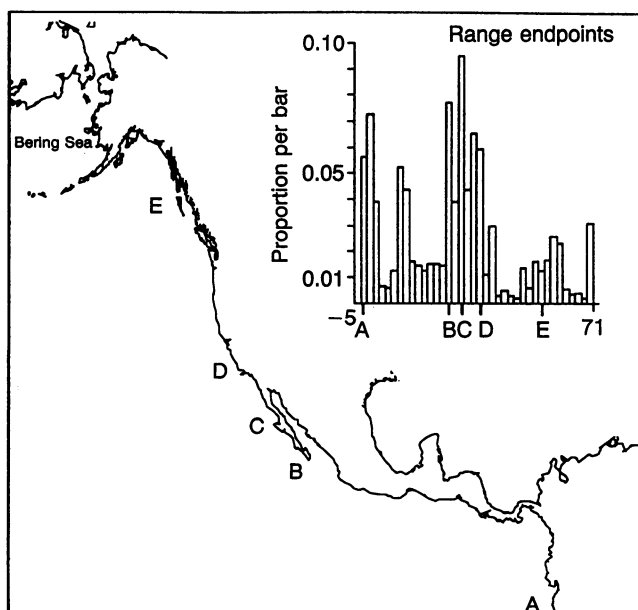

Fig. 2.   Northern and southern range endpoints of 2838 species of eastern Pacific marine mollusks plotted as a function of latitude; each bar represents 2° latitude. The letters represent provincial boundaries of Valentine (24): Paita (A), Cabo San Lucas (B), Cedros Island (C), Point Conception (D), and Dixon Entrance (E).

tend to accumulate more short-ranging endemic species so that the median species ranges computed at the provincial scale show an inverse relation with provincial breadth (Fig. 1*D*); the Panamic province has the lowest median species latitudinal range not because it is tropical but because it spans 28° latitude (or 36° if measured from the head of the Gulf of California). The species of the small Aleutian and Californian provinces have similar median latitudinal ranges, and these values are higher than those of the more extensive Oregonian province that lies between them but smaller than those of the even narrower Surian province to the south. The scatter in Fig. 1*B* occurs because a given 5° band in the large provinces encounters many long-ranging species but only a few of the narrowly restricted ones, except near province boundaries where range endpoints cluster. This explains why the cores of the largest provinces, the Panamic and Oregonian, have the lowest median ranges but contain the highest average ranges when the eastern Pacific is broken up into latitudinal bands rather than provinces. Latitudinal ranges of these mollusks are determined not by the climatic zone in which they occur (i.e., tropical vs. temperate) but more by the spatial distribution of the major oceanographic barriers that control latitudinal extent of provinces.

The relationship between latitudinal range magnitudes and latitudinal position probably depends not only on biogeographic structure (particularly the spacing and strength of thermal and other barriers) but also on historical contingencies such as climatic trends and timing of barrier formation (e.g., see ref. 11). Relative effects of all these factors will vary on a case-by-case basis. This may explain the mixed results of previous analyses of Rapoport's rule. For example, France (11) found increasing mean ranges with latitude for amphipods above 35° N and for crayfish above 20° N but argued that factors such as geological barriers and effects of glaciation may have been more important than simple thermal tolerance. Pagel *et al.* (30) found latitudinal patterns in North American mammals to be consistent with Rapoport's rule but pointed out that correlation of latitude and average range span may not be representative of individual species patterns. Ricklefs and Latham (8) did not find strong support for Rapoport's rule among genera of temperate perennial herbs and neither did Smith *et al.* (9) for Australian mammals. Rohde *et al.* (7) found no evidence for this hypothesis in marine teleosts, and although they found the mean ranges of North American and European freshwater fish to increase with latitude above 40° N, they concluded that Rapoport's rule is not a general explanation of latitudinal diversity gradients. While we agree with their overall conclusions, their analysis of marine teleost ranges involved pooled data from the Indo-Pacific and Atlantic oceans. These two regions could hardly be more disparate in climatic history and biogeographic structure, and as we show here, Rapoport's rule is best tested within a single biogeographic context.

Although the latitudinal gradient is the first-order global diversity pattern, provinciality clearly produces an important second-order effect and has a particularly important influence on latitudinal ranges. Ranges vary with province breadth and not with latitude, which may help to explain why previous attempts to test Rapoport's rule have produced mixed results. Meaningful explanations of latitudinal diversity gradients must take province-scale biogeography into account.

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