Dissecting latitudinal diversity gradients: functional groups and clades of marine bivalves

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The latitudinal diversity gradient, with maximum taxonomic richness in the tropics, is widely accepted as being pervasive on land, but the existence of this pattern in the sea has been surprisingly controversial. This is partly due to Thorson's influential claim that the normal latitudinal diversity gradient occurs in marine epifauna (taxa living on the surface of the substratum) but not in infauna (burrowing or boring into the substratum), a contrast he attributed to the greater spatial and temporal environmental homogeneity of infaunal habitats. In an analysis of 930 species of north-eastern Pacific marine shelf bivalves, we found that bivalves as a whole, and both infauna and epifauna separately, show a strong latitudinal diversity gradient (measured as number of species per degree latitude) that is closely related to mean sea surface temperature (SST), even in analyses of residuals and first differences. This agrees with results for marine gastropods, but contradicts Thorson's environmental homogeneity hypothesis. The relationship between SST and diversity is consistent with a species–energy hypothesis, but the linkages from SST to diversity remain unclear. Most bivalve clades within broad functional groups conform to the general latitudinal trend, except for the deposit-feeding protobranchs. This group's non-directional pattern may be related to its mode of development, because a similar effect is seen in several other groups locked into this low-fecundity, non-feeding larval mode.

Keywords: latitudinal diversity gradient; marine bivalves; species–energy hypothesis

1. INTRODUCTION

One of the most striking of large-scale biotic patterns is the latitudinal gradient in species diversity, peaking in the tropics and tailing off towards the poles. This trend in species richness (which we will refer to as diversity) has been documented for many groups of organisms, both marine and terrestrial, and despite a few exceptional taxa is widely accepted for the biota as a whole (e.g. Fischer 1960; Pianka 1966; Rhode 1992; Gaston 1996; Brown & Lomolino 1998). The diversity gradient is best documented for terrestrial organisms, and for marine organisms in the Northern Hemisphere. Considerable debate remains as to how geographically and taxonomically pervasive the gradient is in the oceans (Clarke 1992; Gaston 1996; Clarke & Crame 1997), and whether the gradient is seen across a wide range of functional groups, such as the marine infauna (burrowers and borers) and epifauna (which live at the surface of the substratum) (Thorson 1952, 1957; Fischer 1960; Clarke & Crame 1997).

Marine molluscs are the most diverse group of shelf macrobenthos, and we have recently documented the Northern Hemisphere diversity gradient in the marine gastropod fauna of both the north-western Atlantic and north-eastern Pacific Oceans (Roy *et al*. 1998). Here we quantify the latitudinal diversity pattern of species of marine Bivalvia in the north-eastern Pacific, from northern Peru to Alaska. We have analysed the bivalve fauna as a whole for comparisons with the gastropod latitudinal diversity trend, and its relationship to temperature as a test of a species–energy hypothesis. We have also taken advantage of the mixture of functional groups represented in Bivalvia to quantify the latitudinal diversity trends in the infauna and epifauna, and among feeding types.

2. ENVIRONMENTAL CONTROLS

In perhaps the most influential challenge to the universality of diversity gradients in the sea, Thorson (1952, 1957) suggested that the regional diversity trend for a major component of the marine biota, the infauna, was independent of latitude. Using diversity data for gastropods, echinoderms and arthropods, he argued that infaunal species are so buffered from spatial and temporal environmental variation by their burrowing habit that their diversity trends should not reflect macroclimate variations, and thus should lack a latitudinal gradient, as opposed to co-occurring epifauna (also see similar comments on bivalves, Thorson (1965)). In contrast, a more recent model of diversity regulation holds that latitudinal trends in diversity are a positive function of available energy rather than an inverse function of environmental variability or harshness (e.g. Wright *et al*. 1993; Fraser & Currie 1996; Turner *et al*. 1996). Results consistent with such a species–energy hypothesis have been obtained in reef corals (Fraser & Currie 1996) and shallow-marine gastropods (Roy *et al*. 1998). However, the former group is entirely epifaunal in habit and the latter predominantly so, which means that these analyses have not directly addressed Thorson's hypothesis that the dominant environmental factors governing latitudinal diversity gradients should only be effective for epifaunal species.

3. METHODS

The database for this analysis consists of the latitudinal ranges of 930 out of the approximately 950 marine bivalve species known from the continental shelf (<200 m depth) from the tropics (5° South) to the Arctic Ocean (71° North) in the north-eastern Pacific. We compiled the data through an exhaustive search of the primary literature as well as from the major museum collections (Jablonski & Valentine 1990; Roy *et al.* 1994, 1998). The extra-tropical data were revised using the excellent volume of Coan *et al.* (2000). Individual species were categorized by life habits using published accounts (e.g. Smith & Carlton 1975; Bernard 1979; Morris *et al.* 1980), and comparisons to similar confamilial taxa where necessary (e.g. Stanley 1970, 1988; Boss 1982).

We use mean sea surface temperature (SST) as a proxy for energy availability (Roy *et al.* 1998; for analogous terrestrial analyses, see Wright *et al.* (1993)). Mean SST values for each degree of latitude from 5° South to 60° North were compiled using a monthly SST data set averaged over a ten-year period between October 1981 and December 1990 (Schweitzer 1993). Regression of these average SST values and diversity was used to test the species–energy relationship. As mean SST and diversity both vary with latitude, we also examined the relationship between mean SST and diversity using residuals from regressions of latitude versus mean SST and latitude versus diversity (Roy *et al.* 1998). Finally, because both diversity and mean SST data show spatial autocorrelation, we calculated the first differences (the difference in values between adjacent latitudinal bins, $X_{i+1} - X_i$) for the two data sets. The correlation coefficient between latitudinally paired first differences for mean SST and diversity provides a test of the species–energy relationship that is not sensitive to the spatial autocorrelation present in the raw data (Ezekiel & Fox 1959).

Species richness can be measured at different scales, from single samples to regional and global biotas (Magurran 1988). A number of previous attempts to assess marine diversity gradients were based on alpha diversities and produced mixed results. These results in turn have generated considerable debate, in part because of the sampling difficulties in single-sample procedures and differences in analytical protocols (see discussions in Boucher & Lambshead 1995; Arntz *et al.* 1997; Clarke & Crame 1997). Here we focus on the number of species that occur in one-degree bands of latitude. Because such data are spatially and temporally averaged, they are relatively robust to sampling and have been used extensively in both marine and terrestrial studies to quantify latitudinal diversity patterns (e.g. Stevens 1989; Rohde 1992). These data are also on the scale used to formulate Thorson's (1952, 1957) original hypothesis on the latitudinal diversity patterns of the infauna and in previous tests of the species–energy hypothesis (Wright *et al.* 1993; Fraser & Currie 1996).

4. RESULTS

Eastern Pacific Bivalvia show a strong latitudinal diversity gradient in the Northern Hemisphere. Within the tropics, species numbers increase from the southern tropical boundary (5° South) to a peak off Panama (8–9° North), and are roughly constant from there to the northern edge of the tropics (23° North), where diversity drops sharply, by about 50% (figure 1). Outside of the tropics, species numbers show a stepwise decline towards
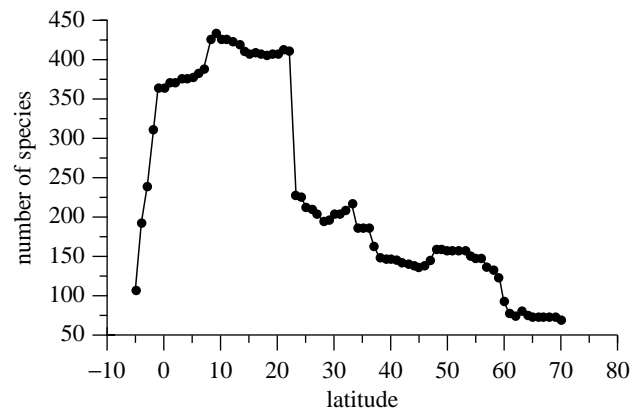
Figure 1. Latitudinal diversity gradient for north-eastern Pacific continental shelf marine bivalves ($n = 930$ species).

the pole, with the steps corresponding to provincial boundaries that form at the boundaries between major water masses or water types (Valentine 1966; Roy *et al.* 1994). This confirms and augments earlier analyses of bivalves in other oceans and at coarser geographical scales (Fischer 1960; Stehli *et al.* 1967). The overall diversity gradient in north-eastern Pacific shelf bivalves is very similar to that documented for shelf gastropods in the north-eastern Pacific, and, remarkably, in the north-western Atlantic as well (for north-eastern Pacific gastropods and bivalves, $p < 0.0001$, Spearman's rank correlation; see Roy *et al.* 1998). Regressions of mean SST and diversity data show a strong correlation along the entire tropics-to-Arctic transect ($r^2 = 0.92$ for all bivalves, 0.91 for infaunal species only, 0.94 for epifaunal species only; see also Bernard *et al.* 1991), but as noted above, this result is not very informative because both variables are themselves correlated with latitude. However, the residuals analysis also shows a highly significant relationship between SST and diversity (figure 2*a*), as do the first differences of mean SST and diversity (figure 2*b*). The strong temperature–diversity relationship documented here is also consistent with the pattern observed for shelf gastropods (Roy *et al.* 1998).

Marine bivalves can be divided into two major functional categories based on their living position: infaunal species that burrow or bore into the substratum, and epifaunal species that are free lying or attached to the surface of the substratum (e.g. Stanley 1988). As noted above, Thorson argued that in the marine macrobenthos, a diversity gradient should be strong only in epifaunal forms, and weak or absent in infaunal, level-bottom forms. However, in our data both epifaunal and infaunal bivalve species show strong latitudinal diversity gradients (figure 3*a,b*). When borers are removed from the infaunal data set, soft-bottom forms (i.e. burrowers only) still show a strong gradient. The ratio of infaunal to epifaunal species shows an overall positive trend with latitude (figure 3*c*), albeit with a possible plateau or gentle decline in the tropics, and an excursion in the northern Bering Sea, where the number of species is so low that the deviation is unlikely to be biologically meaningful. This trend evidently had the opposite slope in the Late Jurassic (Crame 1996) and the Late Cretaceous (D. Jablonski, unpublished data, from Jablonski & Raup 1995), a
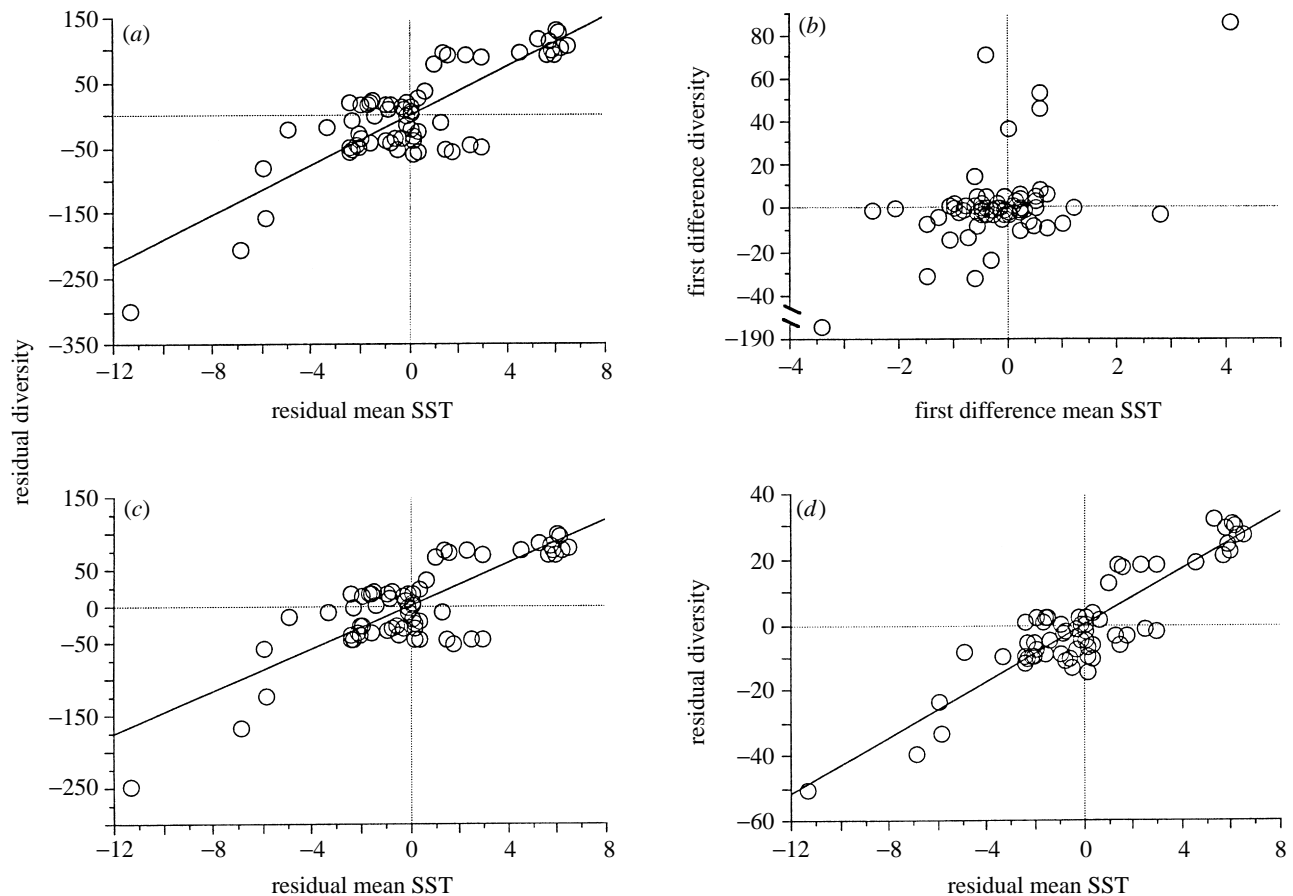
Figure 2. Relationship between species diversity and mean SST for north-eastern Pacific bivalves. Analysis of residuals from the regressions of mean SST versus latitude and diversity versus latitude for (*a*) all bivalves ($r^2 = 0.69$, $p < 0.0001$, $n = 930$ species), (*c*) infaunal bivalves only ($r^2 = 0.65$, $p < 0.0001$, $n = 776$ species), (*d*) epifaunal bivalves only ($r^2 = 0.81$, $p < 0.0001$, $n = 154$ species). (*b*) Relationship between first differences of mean SST and diversity for all bivalves (correlation coefficient = 0.563, $p < 0.0001$). The point at the bottom left corner of the plot marks the sharp change in species richness at Cabo San Lucas ($23°$ N), note the break in scale.

temporal dynamic that merits investigation. In any case, in modern seas mean SST is clearly a good predictor of diversity for both epifaunal and infaunal bivalves, and for soft-bottom dwellers alone (figure 2*c*,*d*).

Position within the trophic web is another important ecological attribute of macrobenthic species, and bivalves can be divided into several trophic categories. Major bivalve categories are suspension feeders and deposit feeders, while minor feeding types include carnivores (septibranchs) and chemautotrophs (e.g. solemyids and lucinids). Both of the major feeding types show strong diversity differences between tropical and extratropical regions, but only suspension feeders show a monotonic decline in diversity from Panama to the Arctic; deposit feeders show a second diversity plateau in extratropical waters (figure 4*b*). As deposit feeders fall chiefly into two major clades, tellinids and protobranchs, we examined each separately. The tellinids, which live within the sediment but collect detritus at the surface and in some instances are facultative suspension feeders (Pohlo 1969; Levinton 1991; Kamermans 1994), show a strong gradient, essentially parallel to that of suspension feeders and their constituent clades such as the venerids (figure 4*c*). Protobranchs, which live and feed entirely within the sediment, show no strong latitudinal trend (figure 4*d*). They do

show a sharp diversity drop at the tropical–extratropical boundary, but in contrast to the tellinids, they regain and maintain tropical levels of diversity in extratropical latitudes.

Species numbers for the minor feeding types are low, and their diversity patterns may have little general importance. Carnivorous bivalves are generally rare and fragile, and live mostly in deep water (Bernard 1974; Poutiers & Bernard 1995). At shelf depths, carnivorous bivalve diversity peaks in the most intensively sampled region, raising the possibility of a sampling artefact (figure 4*f*). Chemautotrophic bivalve diversity peaks in the tropics, but the diversity pattern is noisy and may reflect small numbers and/or the patchy distribution of favourable habitats (figure 4*e*).

5. DISCUSSION

The results presented here provide additional support for the presence of a strong latitudinal diversity gradient in the marine shelf benthos, and are highly congruent with diversity trends documented for gastropods along both the north-western Atlantic and north-eastern Pacific shelves (Roy *et al.* 1998). The ecological and evolutionary processes that underlie the gradient are still unclear,
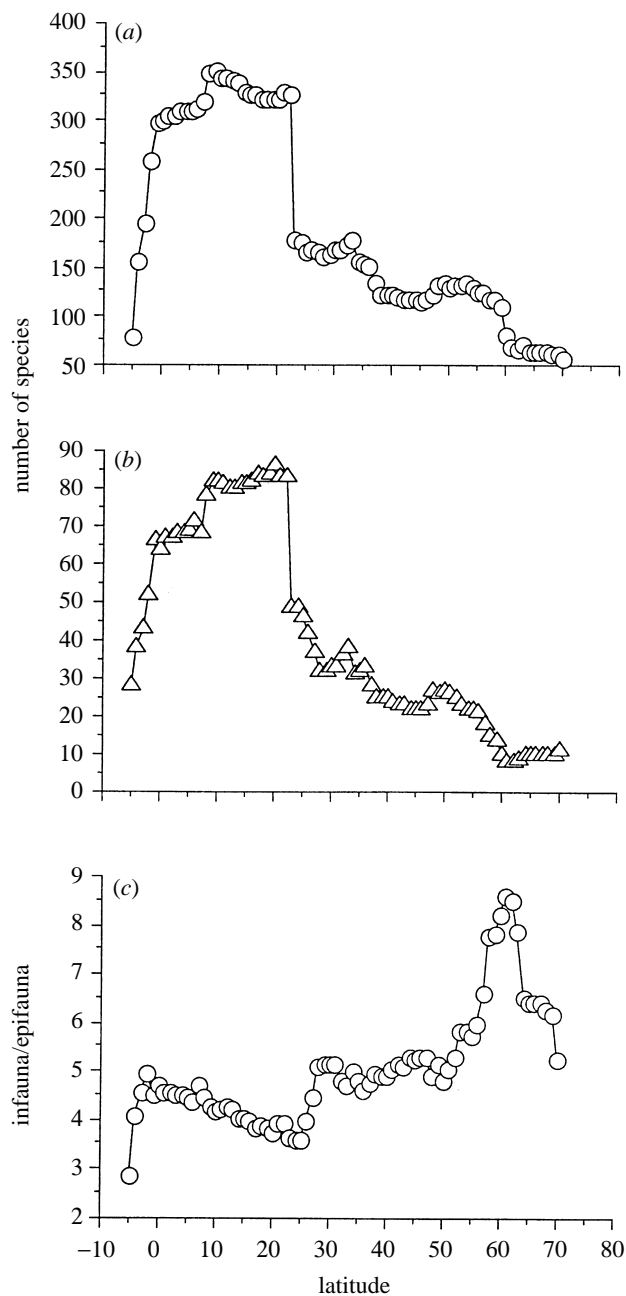
Figure 3. Latitudinal diversity gradient of (*a*) infaunal and (*b*) epifaunal north-eastern Pacific bivalves. Both groups are characterized by a strong decline in diversity from the tropics to the pole, contrary to Thorson's hypothesis. (*c*) Latitudinal trend in the ratio of infaunal versus epifaunal bivalves along the north-eastern Pacific.

although a number of hypotheses have been proposed (Pianka 1966; Valentine 1983; Rhode 1992; Rosenzweig 1995; Gaston 1996; Brown & Lomolino 1998). Our results are consistent with a growing body of evidence that energy-related variables may indeed be a good predictor of the latitudinal diversity gradient in both marine (Fraser & Currie 1996; Roy *et al.* 1998) and terrestrial systems (Turner *et al* 1996; Wright *et al.* 1993), although the processes that link energy input to diversity remain unclear (see the discussion in Wright *et al.* (1993)) and may be indirect. Incident solar energy is a simple function of latitude (e.g. Barry & Chorley 1992), whereas SST is a complex function of climatic variables, ocean circulation

and other factors. For example, negative temperature anomalies with respect to latitude along the north-eastern Pacific coast often accompany seasonal upwelling cells, while positive temperature anomalies can be associated with stable pools of protected waters (Hill *et al.* 1998). These local variations in ocean circulation in turn can affect the timing and quantity of nutrient availability. Thus the strong relationships shown in figure 2 are equally consistent with the view that seasonal stability of trophic resources may also be an important control on diversity (e.g. Valentine 1983). However, further tests of this hypothesis using data on primary productivity at the appropriate geographical scale are needed.

The strong latitudinal diversity gradients in both infaunal and epifaunal molluscan species are inconsistent with Thorson's (1952, 1957) hypothesis that environmental buffering controls the latitudinal patterns of infaunal species diversity. While marine infaunal habitats might provide some buffering against climatic variation within marine sediments, this may be offset by heightened variations of redox conditions, metabolite concentrations and other biogeochemical factors relative to epifaunal habitats (Aller 1994; Boudreau & Marinelli 1994; Forster 1996). Even if Thorson's predicted contrast between infaunal and epifaunal environmental stability holds, local environmental heterogeneity has been rejected as a mechanism behind latitudinal diversity gradients for a number of terrestrial groups, from ants to mammals (Davidowitz & Rosenzweig 1998).

Sanders (1968) was evidently the first to challenge Thorson's hypothesis, but his results were challenged in turn because the data were derived from a variety of sampling protocols (see, for example, Abele & Walters 1979*a*,*b*; Warwick & Ruswahyuni 1987). Subsequent studies have failed to reach a consensus. Kendall & Aschan (1993) found no significant differences in diversity among shallow-water tropical, temperate and arctic sublittoral sites (see also Richardson & Hedgpeth 1977; Warwick & Ruswahyuni 1987; Coates 1998). On the other hand, Rex *et al.* (1993, 1997) found a latitudinal diversity gradient in deep-sea bivalves, gastropods, and isopods (but see Brey *et al.* (1994) and responses by Rex *et al.* (1997)). Part of the difficulty in interpreting some of these data is that the samples have chiefly measured alpha or local diversity, which are widely used but do 'not necessarily provide insight into regional or biotope species pools' (Boucher & Lambshead 1995, p. 1602). If alpha diversity does not vary across latitudes, then the major diversity gradients documented here must be accommodated by beta diversity, that is, by differences in spatial or temporal turnover of species. Such patterns cannot be measured in single samples; as beta diversity increases, samples must be pooled on increasingly large scales to capture regional diversity (Harrison *et al.* 1992; Cornell & Karlson 1997; Srivastava 1999). Our regional diversity patterns provide a framework for testing the hypothesis of increasing beta diversity towards lower latitudes.

Protobranch bivalves are an exception to the strong overall latitudinal gradient seen in our data. One might argue that these subsurface deposit feeders are exploiting food sources that are not dependent on solar energy input, but recent work has increasingly tied production and maintenance of deposit feeders, including those
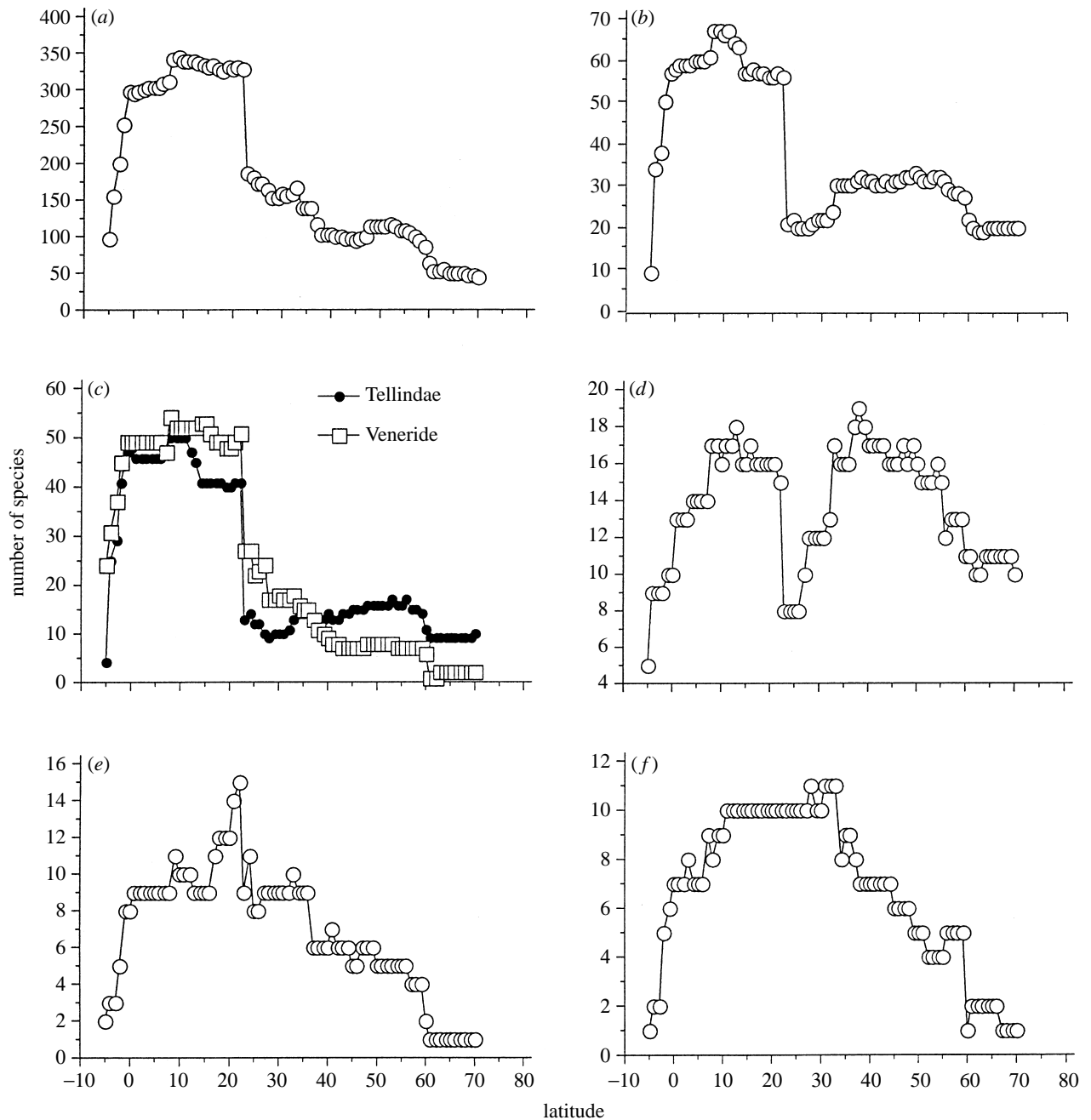
Figure 4. Latitudinal diversity gradient in different functional groups of north-eastern Pacific bivalves. When we partition deposit feeders (*b*) phylogenetically, the tellinid trend more closely resembles that of the venerids (*c*) or suspension feeders as a whole (*a*), whereas deposit-feeding protobranchs (*d*) do not show a strong gradient.

feeding at depth within sediments, to surface productivity even in the deep sea (Levinton 1996; Rex *et al.* 1993, 1997). Another possibility is that the species-level systematics of shallow-water protobranchs have lagged behind that of other groups, and few would question that protobranch systematics deserve more attention. Alternatively, protobranch diversities may be related to their reproductive and developmental strategy, a relatively low-fecundity, non-feeding mode of development known as non-planktotrophy (Scheltema 1994). Groups locked into non-planktotrophic development, which may or may not include a free-swimming stage, often fail to conform to a latitudinal diversity gradient, a tendency noted for articulate brachiopods and several other invertebrate clades

(Valentine & Jablonski 1983). More generally, biotas in high latitudes are rich in non-planktotrophic species (Jablonski & Lutz 1983; Pearse *et al.* 1991; Hain & Arnaud 1992; Pearse 1994). In contrast to the shelf fauna, deep-sea protobranchs do show a latitudinal diversity gradient (Allen & Sanders 1996, Rex *et al.* 1997). However, the deep-sea bivalve fauna is dominated at all latitudes by taxa having low-fecundity, low-dispersal reproductive modes (except perhaps around seeps and vents; Gustafson & Lutz 1994; Tunnicliffe *et al.* 1998), so that the protobranchs would enjoy similar advantages at all latitudes and other factors can govern diversity trends.

This reproductive-mode hypothesis is difficult to test rigorously because most of the data come from taxa

confined to a single developmental mode and other clade-specific factors may come into play. However, marine decapod crustaceans with planktotrophic larvae conform to the latitudinal gradient (Lindley 1998) whereas the caridean decapods and the amphipod crustaceans, characterized by brooding, benthic reproduction, do not (Myers 1996; Lindley 1998). A similar test is needed for molluscan clades that contain both developmental modes and would be particularly informative if reproductive types are tracked over evolutionary time using fossil larval shells (Jablonski & Lutz 1983).

6. CONCLUSION

Our results show that a strong latitudinal diversity gradient is present in the north-eastern Pacific ($5° S–71° N$) not only for marine bivalves as a whole but also for the major functional groups of bivalves. Separating certain functional groups into clades, however, shows that individual clade patterns may vary and be masked by broad functional categories, as with deposit feeders. The overall gradient closely resembles that of marine gastropods. Our data, along with those for marine gastropods and reef corals, provide strong support for a relationship between diversity and energy-related variables although the processes that link the solar energy supply to diversity remain unclear, and indirect effects related to productivity may be important. If diversity regulation is ultimately tied to productivity, then the seasonality of energy supply and the regimes of nutrient supply and depletion are likely to play important roles (Valentine 1983). Further comparative studies among regions, clades and functional groups are needed to resolve this problem.

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