



Patterns of diversity, depth range and body size among pelagic fishes along a gradient of depth

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ABSTRACT

Studies of geographical patterns of diversity have focused largely on compiling and analysing data to evaluate alternative hypotheses for the near-universal decrease in species richness from the equator to the poles. Valuable insights into the mechanisms that promote diversity can come from studies of other patterns, such as variation in species distributions with elevation in terrestrial systems or with depth in marine systems. To obtain such insights, we analysed and interpreted data on species diversity, depth of occurrence and body size of pelagic fishes along an oceanic depth gradient. We used a database on pelagic marine fishes native to the north-east Pacific Ocean between 40°N and 50°N. We used data from the Pacific Rim Fisheries Program that were obtained from commercial, management and scientific surveys between 1999 and 2000. Depth of occurrence and maximum body length were used to assess the distributions of 409 species of pelagic fishes along a depth gradient from 0 to 8000 m. A presence–absence matrix was used to classify the depth range of each species into 100-m intervals. Atmar & Patterson's (1995) software was used to quantify the

degree of nestedness of species distributions. Pelagic fish species diversity decreased steeply with increasing depth; diversity peaked at less than 200 m and more than half of the species had mean depths of occurrence between 0 and 300 m. The distribution of species showed a very strong nested subset pattern along the depth gradient. Whereas species with narrow ranges were generally restricted to shallow waters, wide-ranging species occurred from near the surface to great depths. The relationship between maximum body size and mean depth range differed between teleost and elasmobranch fishes: being positive for teleosts, but negative for elasmobranchs. Results support hypotheses that some combination of high productivity and warm temperature promote high species diversity, and reject those that would attribute the pattern of species richness to the mid-domain effect, habitat area, or environmental constancy. The data provided a clear example of Rapoport's rule, a negative correlation between average depth range and species diversity.

Key words Depth gradient, diversity, geographical range, macroecology, marine ecology, Pacific Ocean, pelagic fish, Rapoport's rule, species richness.

INTRODUCTION

The distribution of species within and among regions of the globe has long been of interest to biogeographers. Much attention has focused on geographical gradients of species diversity, range size and body size. The result has been documentation of several macroecological patterns that describe variation within and among species. The study of these emergent properties has centred largely on terrestrial systems, although recent advances in technology have provided better data on marine

environments, allowing investigators to search for general patterns and processes that are similar across multiple systems. This paper contributes to our understanding of the distribution of marine organisms, and lends insight into the similarities and differences in patterns along terrestrial and marine gradients. We document patterns of species diversity, depth of occurrence and body size that characterize a pelagic fish assemblage along a depth gradient in the north-east Pacific Ocean.

Diversity

Research on terrestrial systems has revealed patterns of diversity along gradients of latitude and elevation (Stevens, 1989; Currie, 1991; Rohde, 1992; Brown, 1995, 2001; Heaney,

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2001; Lomolino, 2001; Md. Nor, 2001; Sánchez-Cordero, 2001). Whereas the latitudinal pattern of species richness in most taxa is a continuous — but not necessarily linear — decline from the equator to the poles (Stevens, 1989; Currie, 1991; Rohde, 1992; Brown, 1995), the elevational pattern is often characterized by a peak in diversity at some intermediate level (Brown, 2001; Heaney, 2001; Lomolino, 2001; Md. Nor, 2001; Sánchez-Cordero, 2001). Recent studies indicate that similar patterns exist in marine environments. Deep-sea bivalves, gastropods, isopods and teleost and elasmobranch fishes show a clear decline in diversity with increasing latitude in the North Atlantic (Rex *et al.*, 1993; Macpherson & Duarte, 1994). Analogous to the elevational gradient in terrestrial systems, species diversity of marine organisms frequently peaks at intermediate depths. This is the case for benthic fishes and gastropods, which are most diverse at mid-bathyal depths in the north-west Atlantic (Rex *et al.*, 1997; Rex & Etter, 1998). The depth distribution of pelagic species is less well understood, although one early report suggests a decrease in pelagic fish diversity with depth along the coast of Oregon (Day & Pearcy, 1968).

Patterns of diversity along gradients of elevation and depth are similar in several ways. Both gradients show continuous, unambiguous trends in some environmental variables, such as atmospheric or water pressure, but potentially more complicated patterns in other variables, such as productivity and physical heterogeneity. Patterns of species richness are often described by hump-shaped curves, so that peak diversity occurs at some intermediate level (Rex *et al.*, 1997; Rex & Etter, 1998; Brown, 2001; Heaney, 2001; Lomolino, 2001; Md. Nor, 2001; Sánchez-Cordero, 2001). Such hump-shaped patterns of diversity may be due to the occurrence of favourable environmental conditions, such as maximal productivity, near the middle of the gradient. Alternatively, they might potentially be due to a mid-domain effect: the tendency for overlap to be highest near the mid-point if species ranges are distributed randomly within some spatial domain (Colwell & Hurtt, 1994; Colwell & Lees, 2000).

Clear exceptions to hump-shaped patterns sometimes occur, especially in cases where species richness decreases continuously from a peak at the low-elevation or shallow-depth end of the gradient (Day & Pearcy, 1968; Patterson *et al.*, 1996; Heaney, 2001; Sánchez-Cordero, 2001; additional examples in Brown & Lomolino, 1998). In these cases, the continual decrease in diversity with elevation or depth often reflects nested-subset distributions of species, in which the increasingly depauperate faunas constitute increasingly small subsets of the richest faunas (Patterson, 1986; Patterson *et al.*, 1996). As such nested subset distributions represent highly ordered patterns, it is unlikely that they could reflect random distributions of species ranges, so the existence of a high degree of nestedness implies that the patterns of distribution and diversity have been shaped by deterministic processes.

Although it is beyond the scope of this study to draw definitive conclusions about the mechanisms that have produced the patterns, some discussion is warranted. Patterns of species diversity along latitudinal and elevational gradients have sometimes been attributed to historical events, but more often they have been hypothesized to reflect variation in environmental factors such as habitat area, temperature, productivity, abiotic stress or seasonality. It has proved difficult to evaluate the separate or interacting influences of these factors, because most of them show correlated patterns of variation with both latitude and elevation. Pelagic marine systems offer potentially valuable insights, because the above factors do not vary in the same way with depth in the ocean as they do with elevation or latitude on land. Thus, temperature, productivity and daily and seasonal environmental fluctuations decline rapidly with depth. Pressure, a potentially important abiotic stress, increases with depth. In addition, there is a much greater volume of water (the equivalent of area in the three-dimensional marine realm) with similar environmental conditions — dark, cold, high-pressure — at abyssal depths than at the surface (Pickard & Emery, 1982; Lalli, 1999).

A number of studies have linked patterns of marine species diversity to the above environmental factors, especially productivity and temperature. Several authors have related species diversity to productivity (e.g. Day & Pearcy, 1968; Rex *et al.*, 1997). Except for a few specialized groups, such as hydrothermal vent inhabitants, marine organisms depend ultimately on photosynthesis, which is limited to surface waters where there is sufficient penetration of sunlight for phytoplankton or macrophytes to photosynthesize (Lalli, 1999; Pough *et al.*, 1999). Below these surface waters, availability of trophic energy declines rapidly, and organisms must depend on the fall of organic material, mostly detritus, from the surface. It has also been suggested that temperature plays a direct role, perhaps affecting species diversity by influencing the rate of speciation (Rohde, 1992). Temperature has been implicated in the pattern of zooplankton diversity, which is correlated closely with sea-surface temperature and decreases rapidly with depth (Rutherford *et al.*, 1999).

We analyse data on the distributions, species richness and degree of nestedness with respect to depth to evaluate the extent to which the pattern of diversity in pelagic marine fishes is consistent with above hypotheses. Given the observations of other groups in other gradients, pelagic fish diversity would be expected to exhibit either a hump-shaped pattern or a nested subset pattern of decreasing diversity with increasing depth.

Range size

Stevens (1989) coined the term 'Rapoport's rule' to describe the phenomenon that in tropical latitudes, where species diversity is highest, species tend to have restricted geographical ranges. To explain Rapoport's rule, Stevens (1989) suggested

that the annual range of climatic conditions experienced by an organism favours the evolution and maintenance of climatic tolerance. He called this the seasonal variability hypothesis (Stevens, 1989). Stevens also described an elevational equivalent of Rapoport's rule by observing that low-elevation organisms tend to have more restricted elevational ranges than high elevation organisms, supporting further the seasonal variability hypothesis (Stevens, 1992).

Analysis of the latitudinal range of marine teleosts in the Indo-Pacific and Atlantic Oceans did not support Rapoport's rule (Rohde & Heap, 1996). In that study Rohde & Heap (1996) considered latitude alone, but Stevens (1996) combined depth and latitude to measure geographical range, found a bathymetric equivalent of Rapoport's rule, and again suggested seasonal variation as a causal mechanism. These opposing results may be explained partially by the physical properties of temperate-zone marine environments, where surface waters experience extreme seasonality, but there is little annual variation in temperature change below 200 m (Pickard & Emery, 1982; Lalli, 1999). Within the tropics and temperate zones, the vertical temperature gradient is much steeper than the latitudinal gradient: for example, water temperature at the equator may drop from 25 °C at the surface to 5 °C at a depth of 1 km, but it may be necessary to go 5000 km north or south to reach a latitude where the surface temperature has fallen to 5 °C (Pickard & Emery, 1982; Stevens, 1996).

This paper documents the distribution of pelagic fishes along the depth gradient. If the seasonal variability hypothesis holds for the depth gradient, pelagic fishes should exhibit narrow depth ranges in stable deep waters and broader depth ranges in seasonally fluctuating shallow waters. If, on the other hand, range size is correlated inversely with species richness and richness is highest in the warm, productive surface waters, then depth ranges should be narrowest for shallow-water species and this might contribute to a nested subset pattern of species distributions.

Body size

Species body size distributions are an important component of community structure (May, 1986; Blackburn & Gaston, 1994; Brown, 1995). Although we have learned a good deal about body size patterns in terrestrial systems, we know much less about such patterns in marine environments (but see Roy *et al.*, 2000; Roy & Martein, 2001). Early studies in the deep-sea revealed a shift toward smaller average size with increasing depth. Later studies revealed variable and conflicting results. Studies on echinoderms, nematodes, molluscs and benthic fishes have reported positive, negative or no relationship between body size and depth (Pfannkuche, 1985; Jensen, 1988; Fujita & Ohta, 1990; Rex & Etter, 1998). Given these results, it remains unclear if there are general trends in body

size with depth in marine systems. Using maximum body length, this paper analyses the size distribution of major groups of pelagic fishes along the depth gradient.

METHODS

Pelagic fishes native to the north-east Pacific Ocean between 40°N and 50°N were selected for analysis. The Pacific Rim Fisheries Program (PRFP) provided a relatively complete and reliable database, with information on 409 species, representing 73 families and 12 orders. Data on body size and depth of occurrence of each species were compiled by the PRFP, based on commercial, management and scientific trawls that took place in 1999 and 2000. Minimum and maximum depth of occurrence of each species was used to determine: (1) mean depth of occurrence: the average of the two values, and (2) depth range: the difference between the minimum and maximum values. We assumed that a species occurred at all depths between its minimum and maximum depth records. Maximum body length was used as an estimate of body size.

Bathymetric classification was used to determine the number of species found in all combinations of the traditionally recognized depth zones: euphotic 0–166 m, mesopelagic 166–1000 m, bathypelagic 1000–3333 m and abyssal 3333–12000 m. Each species was assigned to the bathymetric zone, or combinations thereof, to which it was restricted. Numbers of species occurrences within 100-m depth intervals were compiled to determine the pattern of pelagic fish species diversity along the depth gradient.

To determine if the distribution of pelagic fishes exhibited a nested subset pattern along the depth gradient, we used the software of Atmar & Patterson (1995). The program calculates disorder as departure from perfected nestedness in a presence–absence matrix of species occurrences. System disorder is expressed in terms of 'temperature' (T), where $T = 100^\circ$ represents complete randomness and $T = 0^\circ$ represents complete order and thus perfect nestedness. The depth gradient was partitioned by 100-m intervals between 0 and 8000 m. Each species was represented as present or absent in each of the 80 depth intervals, and each species was assumed to be present in all of the depth intervals between its minimum and maximum recorded depth of occurrence (as above). A Monte Carlo simulation was used to evaluate the null hypothesis that the matrix was randomly filled subject to constraints on the marginal values (Atmar & Patterson, 1995).

RESULTS

Diversity

Pelagic fish diversity showed a significant decrease with increasing depth ($P < 0.0001$) (Fig. 1a). Species richness increased slightly from 0–100 m to 100–200 m, but then declined

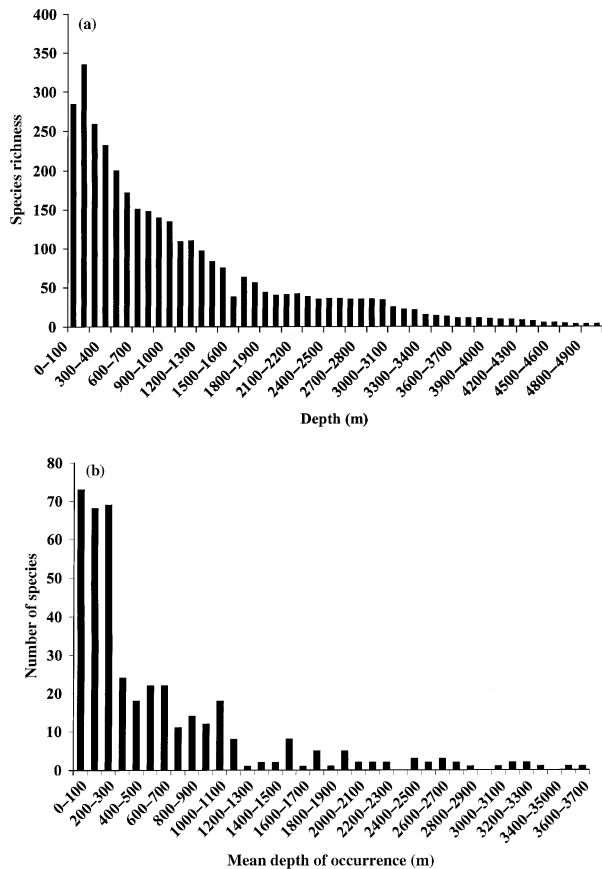


Fig. 1 (a) Relationship between species richness and depth for pelagic marine fishes between 40°N and 50°N in the north-east Pacific Ocean ($P < 0.0001$). Number of species occurrences were summed for 100 m depth intervals between 0 and > 5000 m. (b) Frequency distribution of pelagic marine fishes along the depth gradient between 0 and 6200 m. Species were sorted into 100-m depth intervals based on mean depth of occurrence.

rapidly with increasing depth. More than half the 409 species occurred in shallow water between 0 and 300 m, while fewer than 25 species occurred at depths greater than 3000 m.

Depth range

Expressing the same data in a somewhat different way, mean depth of occurrence of the species also declined rapidly with depth, from a peak at 300 m to an eventual levelling-off in deep waters ($P < 0.001$) (Fig. 1b). Species with narrow depth ranges were restricted to the euphotic and/or mesopelagic zones, while those that had wide depth ranges occurred typically in these near-surface zones but also ranged as deep as the bathypelagic and abyssal zones (Fig. 2). Fully 61% of the species were restricted to the euphotic and mesopelagic zones, whereas fewer than 5% were restricted to the bathypelagic

and abyssal zones. Only 20 species had a minimum depth of occurrence in waters deeper than the mesopelagic zone, and only four species ranged across all depth zones (Table 1 and Fig. 2).

The distribution of pelagic fishes along the depth gradient exhibited a highly nested subset pattern (Fig. 2). The temperature, $T = 2.44^\circ$, estimated by the Atmar & Patterson (1995) calculator makes this one of the most highly nested assemblages ever recorded. The probability (P) of obtaining such a high degree of nestedness by chance alone, calculated by the software of Atmar and Patterson, is $P \lll 10^{-12}$. This value may be too low, because we assumed that each species was distributed in all depth intervals between its minimum and maximum records, whilst the nestedness calculator assumes that a presence or absence can be randomly assigned to any sample (depth interval). Nevertheless, the probability that such an extreme degree of nestedness could occur by chance is vanishingly small.

The inverse relationship between depth range and species richness is consistent with Stevens's (1989, 1992, 1996) formulation of Rapoport's rule. As richness declined with increasing depth, species exhibited ranges that extend over a greater depth range (Fig. 3). The fact that the species with the narrowest ranges occurred in the most seasonally variable environment, however, is contrary to the seasonal variability hypothesis that Stevens proposed as the mechanism for Rapoport's rule.

Body size

The relationship between body size and mean depth of occurrence varied among classes and orders (Fig. 4). There were statistically significant relationships between maximum body length and mean depth of occurrence for seven of the 12 orders, but the direction of these relationships varied. While teleosts exhibited a positive or no relationship, three of the four orders of elasmobranchs revealed an inverse relationship (Fig. 4). The relationship between body size and depth range also varied between teleosts and elasmobranchs (Fig. 5). There was a significant inverse relationship between maximum body length and depth range for elasmobranchs, so that the smallest species occurred over the greatest range of depths (Fig. 5). Teleosts, however, exhibited a positive trend, where the largest species tended to occur over the greatest range of depths (Fig. 5).

DISCUSSION

Diversity and depth

Pelagic fish diversity was highest in shallow waters. The data suggest that species richness was slightly greater between 100 and 200 m than in the shallowest interval, 0–100 m. This

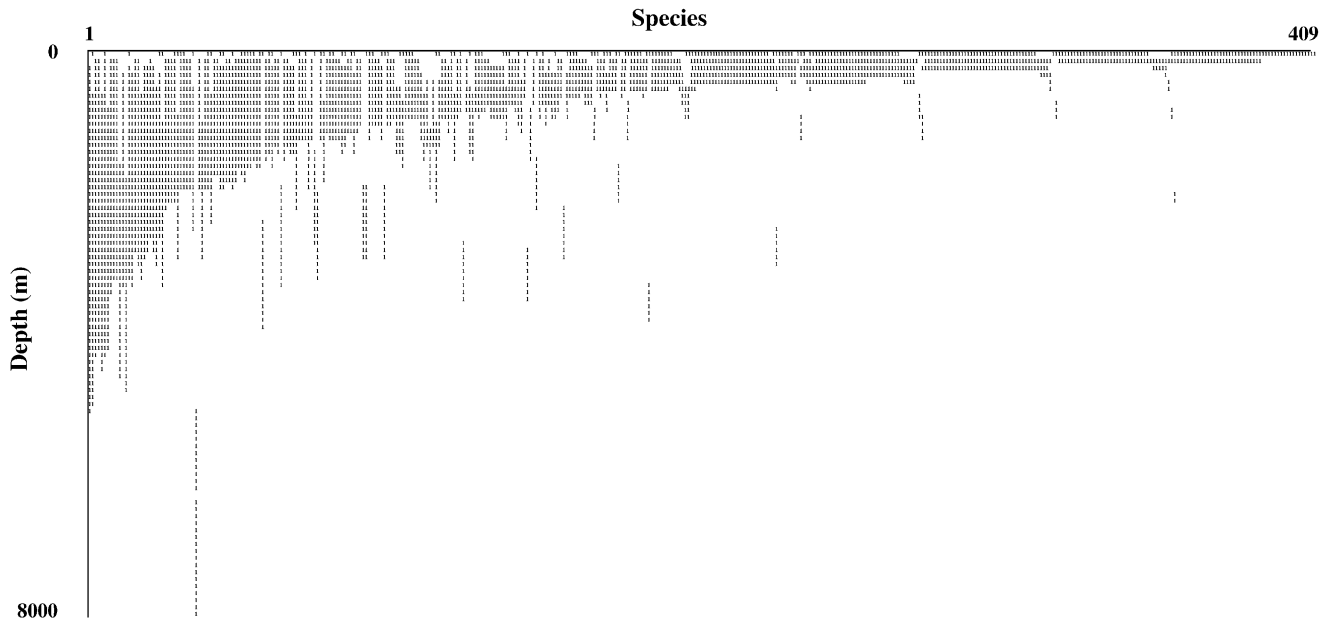


Fig. 2 Nested depth distribution of pelagic marine fishes between 40°N and 50°N in the north-east Pacific Ocean. Vertical dashed lines represent depth of occurrence for each species along a depth gradient divided into 100-m intervals between 0 and 8000 m.

Table 1 Number of pelagic marine fish species restricted to bathymetric depth zones between 40°N and 50°N in the north-east Pacific Ocean

Zone	Depth (m)	Number of species
Euphotic	0–166	69
Euphotic–Mesopelagic	0–1000	180
Euphotic–Mesopelagic–Bathypelagic	0–3333	52
Euphotic–Mesopelagic–Bathypelagic–Abyss	0–12000	4
Mesopelagic	166–1000	30
Mesopelagic–Bathypelagic	166–3333	49
Mesopelagic–Bathypelagic–Abyss	166–12000	5
Bathypelagic	1100–3333	12
Bathypelagic–Abyss	1100–12000	6
Abyss	3333–12000	2

pattern may be a real feature of marine diversity, reflecting the influence of environmental conditions on the depth distributions of pelagic fishes. Several factors could be involved, including intense predation under high illumination or constraints on physiological adaptations to the high and variable temperatures, low pressures and high light levels of the shallowest waters. Alternatively, the apparent peak in diversity at 100–200 m may be due to sampling error. Since most of the species in the sample are rare species, they may not have been recorded at all depth intervals where they occurred. Our procedure of assuming that each species occurred at all depths between its minimum and maximum record of occurrence ‘corrects’ for incomplete sampling within the documented depth range. However, the range of a rare species could be

underestimated because it did not appear in one or more samples at the edges — either upper, lower, or both — of its depth range. Such incomplete sampling may account for the apparent absences of some species between 0 and 100 m. It also means that the maximum depth of occurrence for some species may have been underestimated, so that depth ranges and total diversity in the bathypelagic and abyssal zones may be somewhat greater than our analyses suggest. It is inconceivable, however, that such limitations of sampling could alter the general pattern that species richness decreases approximately exponentially with increasing depth.

The dramatic peak in species richness and the concentration of narrow-ranged species in shallow waters show that there is no mid-domain effect: a peak in range overlaps and species

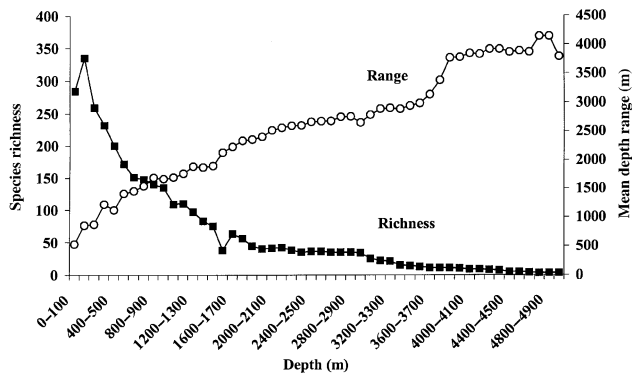


Fig. 3 Species richness and mean depth range plotted as a function of depth (after Stevens, 1989, 1992, 1996) depicts the Rapoport effect for pelagic marine fishes along a gradient of depth.

diversity near the centre of the gradient (Colwell & Hurtt, 1994; Colwell & Lees, 2000). The mid-domain effect is a null hypothesis, which implies that hump-shaped patterns of species diversity could result from species ranges being distributed randomly within a gradient. We can reject this hypothesis emphatically. Not only is the apparent peak in species richness at 100–200 m far from the mid-point of the gradient (Fig. 1a), but also the extreme degree of nestedness demonstrates that the distributions of the species are highly non-random with respect to depth. The vast majority of species occurred in shallow waters, and a large portion of these were restricted to a very narrow range of surface waters. Those species that ranged to progressively greater depths tended to be a subset of those that occurred in more shallow waters. There are other cases, similar to pelagic fishes, where species diversity is concentrated at one end of a gradient due to a nested subset distribution of species ranges. For example, along an elevational gradient in Peru, bat species richness was highest at the lowest elevation and the distributions of species were also highly nested (Patterson *et al.*, 1996; see also Day & Percy, 1968; Sánchez-Cordero, 2001). Such patterns suggest that, at least in these cases, species diversity is strongly influenced by ecological factors that limit the ranges of individual species.

The inverse relationship between pelagic fish species diversity and depth supports hypotheses that implicate temperature, productivity, or both as causal mechanisms. Figure 6 shows the depth profiles for temperature and for plankton biomass, which can be taken as an index of productivity (Longhurst, 1998). Similar to the distribution of pelagic fishes, temperature and plankton biomass decline approximately exponentially with depth, gradually levelling off as depth increases toward the abyss (compare Figs 1 and 4). On closer inspection, however, species diversity appears to remain relatively constant from the surface to approximately 300 m, while temperature and plankton biomass decline more rapidly:

temperature from about 120 m and plankton biomass from about 100 m, but comparisons of these patterns are complicated by seasonal trends, vertical migration of both fish and plankton, and sampling issues (see above). The overall large-scale correlations between fish species diversity and both temperature and plankton biomass are very strong. The fact that temperature and productivity are so highly correlated, however, makes it impossible for our analyses to distinguish between these two factors as possible causes of the rapid decline in pelagic marine fish diversity with depth.

The depth distribution of pelagic fishes fails to support other hypotheses for geographical patterns of diversity. Note that rejection of these hypotheses for pelagic marine fishes does not mean that they may not account for at least some of the variation in diversity in other taxa or in other geographical settings. It does mean, however, that these hypotheses cannot provide universal and sufficient explanations for all patterns of diversity. In particular, the pattern rejects the hypothesis that high diversity of marine pelagic fishes is due to large habitat area (e.g. Terborgh, 1973; Rosenzweig, 1992, 1995). In marine and aquatic systems, pelagic organisms are distributed in a three-dimensional space. This contrasts with the essentially two-dimensional distribution of organisms across terrestrial environments. Consequently, the marine analogue of Rosenzweig's habitat area hypothesis for terrestrial organisms would be a positive effect of water volume on species diversity. This was not observed for pelagic fishes. The vast majority of the ocean is composed of the cold, dark, high-pressure environment below 300 m (Longhurst, 1998), but the vast majority of pelagic fish species are confined to the relatively small volume of warm, productive surface water.

The high diversity in surface waters also fails to support hypotheses that invoke environmental constancy as a major factor promoting high species diversity (e.g. Sanders, 1968, 1969; Stevens, 1989, 1992, 1996; Leigh, 1990; Fjeldsa & Lovett, 1997; see also review in Brown & Lomolino, 1998). These hypotheses are based primarily on the negative correlation between species richness and seasonality observed in latitudinal gradients. They are contradicted by the pattern of pelagic fish distribution, where highest species diversity is found in seasonally fluctuating waters between 0 and 200 m. The nested distribution of pelagic fishes is consistent with Rapoport's rule, as described by Stevens (1996), but the seasonal variability hypothesis cannot explain it. This hypothesis would suggest that species with broad depth ranges should inhabit seasonally fluctuating surface waters, while those with narrow ranges should be restricted to the more stable waters of the benthos. Distributions of pelagic fishes along the depth gradient exhibit the opposite effect.

There has been some debate about whether marine fishes obey Rapoport's rule. Stevens (1996) claimed that they do when both latitude and depth are combined to give a measure

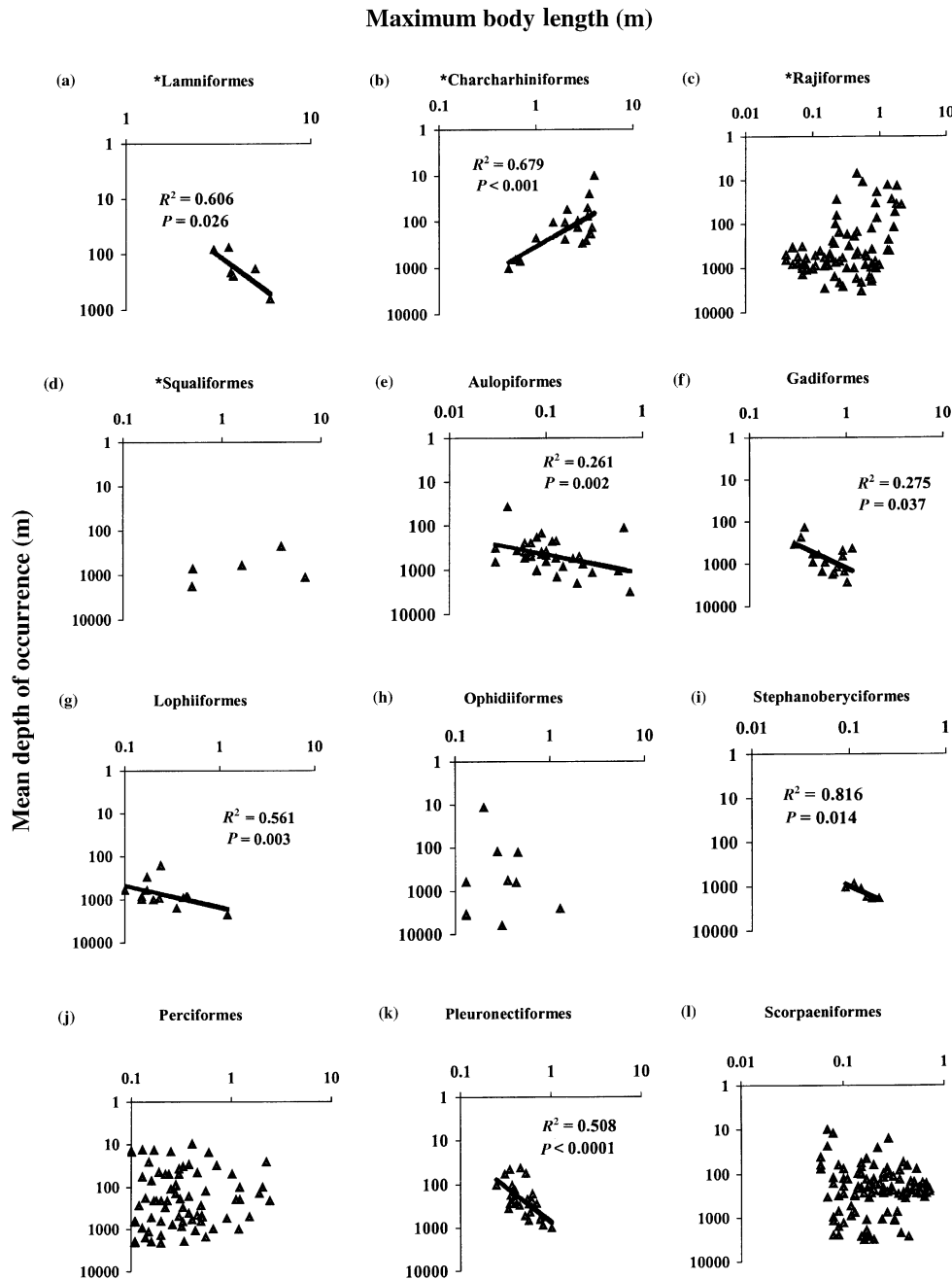


Fig. 4 Mean depth of occurrence–maximum body length relationships plotted on logarithmic axes for 12 orders of pelagic marine fishes. Trend line, r^2 and P -value are depicted for significant relationships. Elasmobranchs are distinguished from teleosts by an asterisk.

of geographical range. Rohde & Heap (1996) examined only latitude and claimed that the Rapoport pattern did not hold for marine teleosts. In this study, we analysed only the depth component of pelagic fish distribution, and found a strong Rapoport phenomenon. Without information on species latitudinal ranges it is unclear whether Rapoport's bathy-

metric rule, as defined by Stevens (1996), holds for this system. However, our results suggest that the inverse relationship between geographical range and species richness is more a consequence of depth than latitude. This outcome further supports the influence of temperature on the distribution of marine species. Recall that the average vertical (depth)

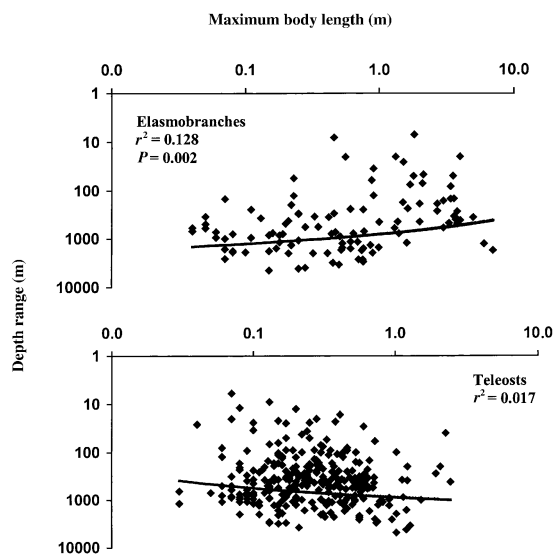


Fig. 5 Depth range–maximum body length relationships plotted on logarithmic axes for pelagic marine elasmobranches and teleosts.

temperature gradient in marine systems is approximately 5000 times the horizontal (latitudinal) one (Pickard & Emery, 1982). This dramatic difference between the depth and latitudinal gradients may explain the opposing results of our study and that of Rohde & Heap (1996). The drastic change in temperature over the shallowest few hundred metres of the depth gradient may be more important in limiting the three-dimensional ranges of pelagic marine species than the much more gradual and seasonally varying change in temperature over hundreds or thousands of kilometres of latitude.

Body size

The nature and causes of size distributions of pelagic fishes along the depth gradient remain unclear. Differences between teleosts and elasmobranches seemed to be relatively consistent, although there were also some differences among orders within these two classes. Given the many differences in morphology, reproduction, feeding strategy, locomotion, and physiology between teleosts and elasmobranches, there are several mechanisms that could account for the differences in body size distributions. Of these, we suggest that differences in reproductive strategy, feeding behaviour, and morphology are likely to be most influential.

With the evolution of internal fertilization, elasmobranches evolved a reproductive strategy favouring the production of a small number of relatively large offspring, retained, protected, and nourished for varying periods of time within the female's body (Pough *et al.*, 1999). This strategy requires substantial investment of maternal energy to each individual offspring. As resource availability decreases with depth (Lalli,

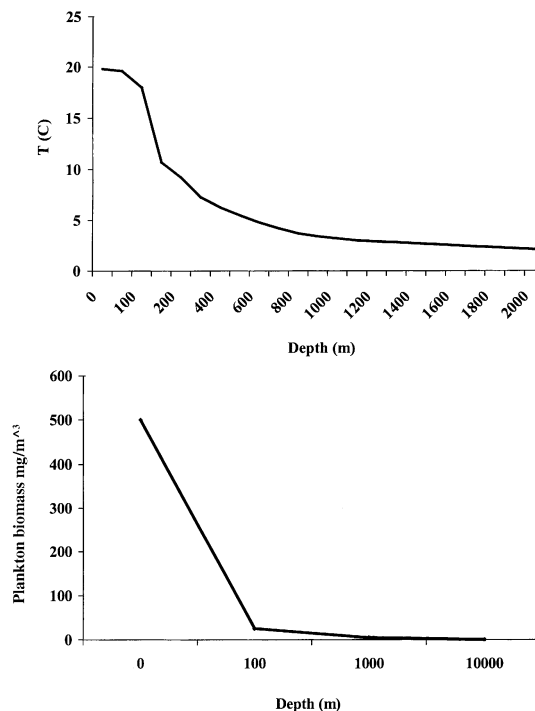


Fig. 6 Depth profiles for average annual temperature and plankton biomass for 40–45°N in the North Pacific Ocean (National Oceanic and Atmospheric Administration). Plankton biomass is used as a surrogate for productivity (Longhurst, 1998).

1999; Pough *et al.*, 1999), investment in offspring becomes even more costly. As a result, selection may favour small elasmobranches in the nutrient-poor waters of the benthos, because their young are given a greater 'head start' than teleosts, many of which have tiny eggs that hatch into planktonic larvae (Pough *et al.*, 1999).

Another common trend in elasmobranches, which is not apparent in teleosts, is the relationship between body size and food resources (Lalli, 1999; Pough *et al.*, 1999). The largest sharks, skates and rays are plankton strainers, whereas piscivores and invertebrate feeders are smaller (Pough *et al.*, 1999). Therefore, the fact that plankton biomass decreases rapidly with depth provides another possible explanation for the shallow-water distribution of the largest elasmobranches (Lalli, 1999; Pough *et al.*, 1999). While whale sharks, manta rays and other large elasmobranches are found in plankton-rich near-surface waters, smaller species such as stingrays and dogfish feed on invertebrates and fish in deep water (Pough *et al.*, 1999).

Coda

Attempts to understand the similarities and differences among patterns of diversity along gradients of latitude, elevation and depth will bring us closer to a general explanation of the

general patterns and processes that characterize global biodiversity. The present study of pelagic fishes along a depth gradient contributes to this goal by presenting four diagnostic patterns of diversity, range and body size:

- 1 Diversity decreases rapidly with depth, from a peak at less than 200 m to very low diversity in the abyss.
- 2 Depth range distributions support Rapoport's rule, being narrowest in species-rich surface waters.
- 3 Depth distributions exhibit a high degree of nestedness.
- 4 Body size–depth range relationships appear to reflect underlying differences between teleosts and elasmobranchs.

Each of these patterns call for further in-depth research into the causal mechanisms of community assembly in marine systems, with special attention to the influence of temperature and productivity. Also important is the need to compare the patterns of distribution and diversity as a function of depth shown here for pelagic marine fishes with patterns in other taxa of pelagic marine organisms, as well as with patterns of species distribution and diversity along other geographical gradients, such as latitude, elevation and water and nutrient availability. Our analysis of the distribution of pelagic fishes along a depth gradient supports hypotheses implicating some combination of temperature and productivity as primary causes of diversity, but it fails to support a mid-domain effect or hypotheses that would assign major causal roles to area (or volume) or environmental constancy.

ACKNOWLEDGMENTS

We thank S. Gaines, J. Gillooly, and M. Lomolino for useful discussion and comments on the manuscript. KFS was supported partially by an NSF Graduate Research Fellowship. JHB gratefully acknowledges the support of a Packard Interdisciplinary Science Grant. This project could not have been conducted without the information compiled by the Pacific Rim Fisheries Program.

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