

Cephalopod species richness in the wider Caribbean region

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The cephalopods of the wider Caribbean region (western central Atlantic) were examined in terms of distribution and ecological importance. In all, 4190 preserved cephalopod specimens were identified and catalogued to produce regional maps of cephalopod distribution within the wider Caribbean. Regional species richness was examined with respect to Rapoport's rule (RR) and to determine possible cephalopod hotspots in the region. Rarefaction curves were used to normalize the samples of various size collected throughout the wider Caribbean. Cephalopods of the wider Caribbean within latitudinal bands from 8 to 30°N do not support RR because they exhibit increasing species richness with increasing latitude. Eight subareas were chosen to compare species richness. Regionally, species richness appears to be patchy, with cephalopods concentrated more off the eastern Florida coast. There is a need for increased sampling throughout the wider Caribbean. Areas were lacking in samples, especially the central and southeastern parts of the region. There is a need to explore the systematics, life histories, and distribution patterns for this group of organisms in future.

Keywords: cephalopod distribution, species richness, wider Caribbean region.

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Introduction

The wider Caribbean region (Figure 1) is defined as the Gulf of Mexico and the coastal and marine areas of the Caribbean Sea, including the chain of islands forming the Greater and Lesser Antilles, Turks and Caicos, The Bahamas, and the Gulf coasts of the United States, Central and South America (Stanley, 1995). The Caribbean Sea proper covers some 2 753 000 km², and the (smaller) Gulf of Mexico some 1 592 842 km². The general circulation is from east to west in the Caribbean and west to east in the Gulf of Mexico, with eddies often spinning off the main water flow (Stanley, 1995; Figure 1).

Fewer than 1000 species of living cephalopods have been described worldwide; >720 are listed in the present catalogues (Jereb and Roper, 2005). Cephalopods are found in all marine habitats, although not at salinity <17.5. Today, they are important in neritic waters, although numerically they constitute just a small part of the shelf fauna. Nearshore, they are generally outnumbered by fish of similar size, except during certain seasons and at some locations. In oceanic waters, they are more diverse in size and play an important role in foodwebs (Clarke, 1996). Their abundance varies depending on group, habitat, and season, from isolated territorial individuals (primarily benthic octopods) through small schools with a few dozen individuals to major schools with millions of oceanic squid (Vecchione, 2002). Their depth range extends from the intertidal zone to deeper than 5000 m. Because of their accessibility, many of the near-surface and coastal cephalopod species of the Greater Caribbean have been studied in detail (Voss, 1956, 1973; LaRoe, 1967; Lipka,

1975; Cairns, 1976; Passarella, 1990). Deep-sea species are more difficult to study because of net avoidance and other escape tactics (Passarella, 1990). A diverse cephalopod fauna is associated with the seabed in both shallow and deep water.

Some 129 cephalopod species are found in the wider Caribbean region (Judkins, 2009). Records of cephalopod species in the Gulf of Mexico date back to Lesueur (1821), but the modern comprehensive systematics of the group begins with Voss (1954, 1956), who reported 24 neritic and oceanic species in his earlier paper and 42 in the later one. Since then, many species have been added to the list (Passarella, 1990).

Although important work has been completed in the wider Caribbean, cephalopod studies have not yet yielded a well-rounded, comprehensive view of distribution and species richness. Various island groups or individual cephalopod species have been addressed, (Díaz *et al.*, 2000; Gracia, 2002; Díaz, 2004) mainly in coastal waters, but to date, no study has described the wider Caribbean species complex as a whole. Rosa *et al.* (2008) and Smith *et al.* (2002) conducted literature-based studies on latitudinal gradients of species richness, but no study has utilized large numbers of specimens from the region to improve our understanding of cephalopod ecology. This paper attempts to fill that need and, based on 4190 specimens, reports diversity trends and cephalopod hotspots in the region.

In addition to comparing cephalopod species richness in the region with that of other studies (e.g. species “hotspots” reported for portions of the wider Caribbean using a wide range of vertebrate and invertebrate species, from Smith *et al.*, 2002), we

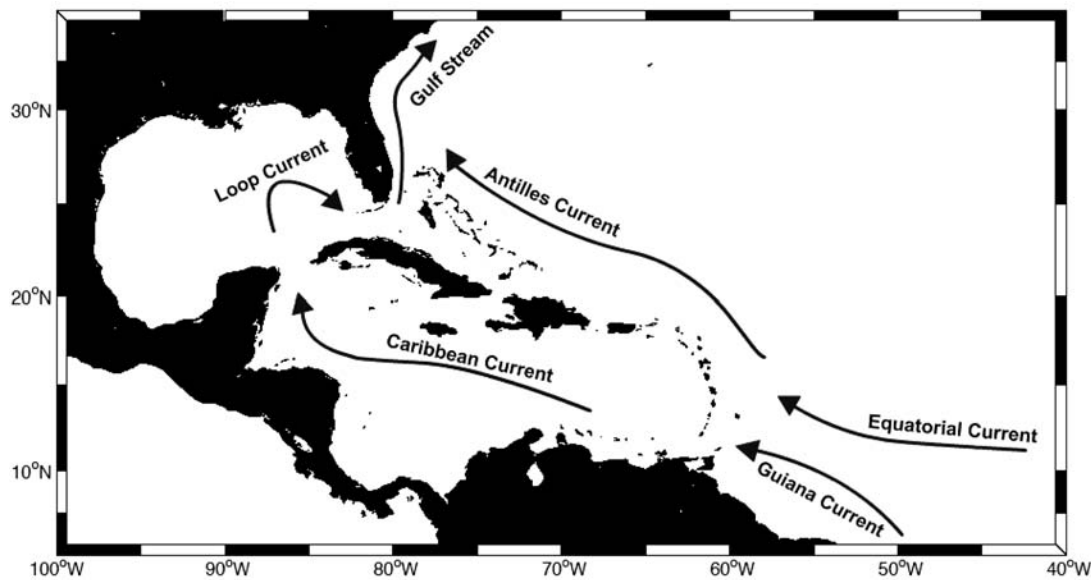


Figure 1. The wider Caribbean region and its currents.

wanted to examine Rapoport's rule (RR) within the latitude range 8–30°N in the area, seeking perhaps an increase in cephalopod diversity at lower latitudes.

Stevens (1989) defined RR as the circumstance in which “when the latitudinal extent of the geographical range of organisms occurring at a given latitude is plotted against latitude, a simple positive correlation is found” (Gaston *et al.*, 1998). Rapoport (1982) had noted that the latitudinal ranges of individual species became smaller in lower latitudes, so more species could be accommodated there because each required less space. Stevens (1989) explained the pattern based on differing tolerances of tropical and temperate species to climatic variations. Organisms inhabiting lower latitudes are subjected to less variation in climate, so their geographical distributions tend to be limited to a narrow climatic range. Higher latitude species would be adapted to more marked climate variation (Fortes and Absalao, 2004). The present research examines RR by focusing on small-scale patterns within a region that had been described as an ecotone. Understanding the application of RR may be essential for conservation and management (Fortes and Absalao, 2004).

Biodiversity to this study is defined as species richness, i.e. the numbers of species per area examined. Correlation of species richness with latitude is found in all higher taxa whose geographical ranges are well known, both terrestrial and marine. Here, we focus on the 22° range of lower latitudes in the wider Caribbean that have not been investigated previously in terms of RR. Biodiversity studies are important to both conservation and sustainable fisheries management, and the information presented here addresses it for cephalopods analysing RR.

The biogeographic pattern proposed by Stevens (1989) has acquired increasing importance among researchers as an explanation for the biodiversity gradient related to latitude (Fortes and Absalao, 2004). Some view RR as a local phenomenon, because many studies do not extend to low latitudes (Gaston *et al.*, 1998). We analyse our data for possible support for RR, not to debate the merits of the concept, as been done often before (e.g. Rohde, 1992; Gaston *et al.*, 1998; Hillebrand, 2004). Since the Gaston *et al.* (1998) review, studies have addressed

both mid- and low latitudes (Macpherson, 2002, 2003; Rosa *et al.*, 2008); many have tested RR, and the outcomes have been mixed. Some authors (Steele, 1988; Roy *et al.*, 1998; Macpherson, 2002) found evidence in their studies supporting RR, whereas others (Clarke, 1992; Mokievsky and Azovsky, 2002) failed to find such a relationship (Rosa *et al.*, 2008). For example, Fortes and Absalao (2004) examined selected bivalves and gastropods along the Pacific and Atlantic coasts of the Americas and attempted to evaluate the applicability of RR in those regions; they concluded that RR did apply there.

Other studies, such as that conducted by Rohde (1992), suggest that RR does not apply to all taxonomic groups. Rohde (1992) focused on marine teleosts using data collected from the Indo-Pacific and Atlantic Oceans and found that RR does not apply in all areas within a taxon's range, concluding that it may be premature to explain greater species numbers by narrower environmental tolerances of tropical species. Many studies have utilized a large range of latitudes (e.g. 80°N to 70°S) for analysis, whereas the present study examines a narrower range, 22° of latitude between 8 and 30°N and from 60 to 95°W, but uses a large sample.

Material and methods

The most reliable taxonomic information comes from examination of actual specimens in conjunction with, but not limited to, data compiled from literature sources. The most helpful taxonomic studies include examination of comparative material from a variety of locations, including where possible from the original type locality (Vecchione *et al.*, 2000). This study used 4190 specimens already collected and in archival collections (Figure 2) to determine the distribution of all cephalopods in the wider Caribbean. Based on the current dichotomous keys for cephalopods (e.g. Voss, 1956; Roper *et al.*, 1984; Nesis, 1987; Vecchione, 2002), examination of type specimens, literature, and expert opinions, they were identified to species level. Most had been preserved well and were in excellent condition, despite some dating back to 1898 (others were relatively new). The bulk of preserved specimens analysed was from two institutions, the Smithsonian

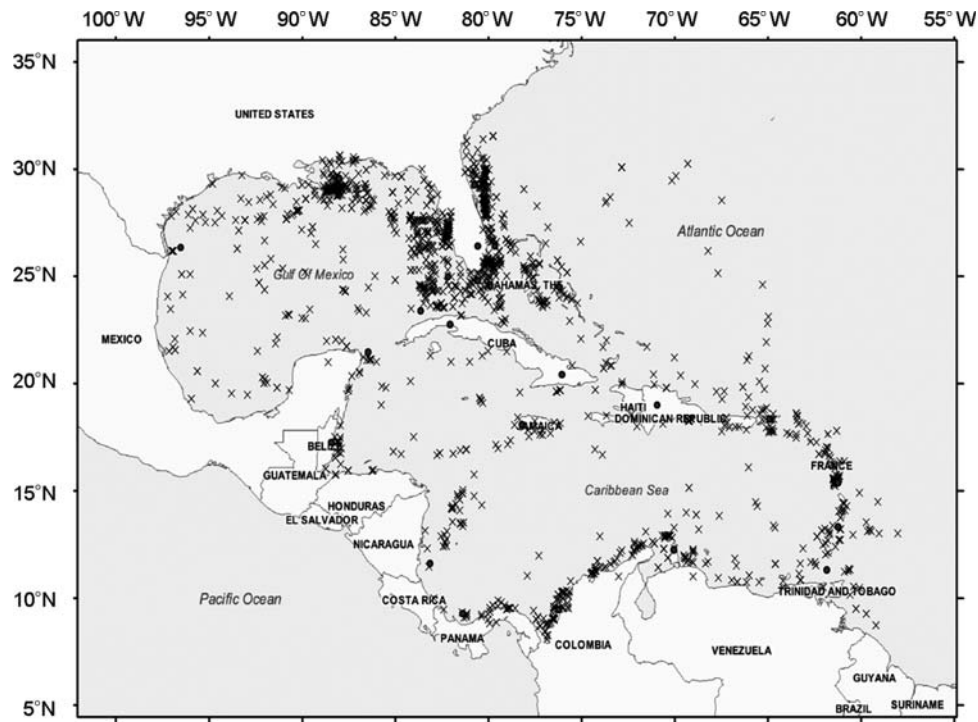


Figure 2. Cephalopod sampling effort, crosses indicating the sites from which samples were derived.

Institution's National Museum of Natural History and the University of Miami Rosenstiel School of Marine and Atmospheric Science. Smaller collections from the Florida Fish and Wildlife Research Institute were also analysed. Hourglass cruises were conducted from 1965 to 1967 in shelf waters off western central Florida, and cephalopod species were identified and documented by R. Toll and S. Hess (unpublished material). Some 500 specimens were included in the present study from those cruises. Once a specimen was identified, it was plotted on a distribution map of the wider Caribbean region using the ArcGIS 9.2 mapping program.

Analysis

RR was evaluated using species richness, which is defined here as species number per 5° latitudinal bin within the study's scope, i.e. 5 bands. This was plotted as species richness against latitude using the number of individuals as well as the number of species. Rarefaction curves were created for all five bands of latitude using Primer 6.2 (Clark and Gorley, 2001). Rarefaction is a tool used to correct for unbalanced sampling structure. The rarefaction curve is produced by repeatedly resampling the pool of n individuals or n samples at random, plotting the average number of species represented by 1, 2, ..., n individuals or samples (Gotelli and Colwell, 2004). It depends on the shape of the species abundance curve rather than the absolute number of specimens per sample.

Rarefaction generates the expected number of species in a small collection of n individuals drawn at random from a large pool of N individuals (Simberloff, 1978). Resampling for the present study equalled 1000 randomizations per latitude bin. After each randomization, samples were drawn and the number of new species recorded. This happened 362 times (x -axis values). Rarefaction can be viewed as the statistical expectation of the

corresponding accumulation curve over different re-orderings of individuals (Gotelli and Colwell, 2004). The method is valid when the same groups of organisms are being compared and contrasted. Another requisite is that all the habitats sampled be similar, such as, in this case, coastal habitats. Methods of capture should be similar, and the method does not specify which species taken from the residue will be present, so it can only be used to interpolate (Sanders, 1968). The rarefaction curves herein are species observed (Sobs) compared with latitude.

The Chao 1 curve, a non-parametric estimator used for species richness comparisons, was used to give the most likely total species estimate for each region based on the actual sample provided. It is based on the number of rare species in a sample and creates an estimate of total species for a region (Magurran, 2004). The two methods, rarefaction and the Chao 1 estimator, verify the raw data (species observed) collected. The trendlines created by both curves should be the focus because they indicate whether or not sample site capacities have been reached. The Sobs graph accounts for sample size differences, and the Chao 1 estimates an absolute number for species richness in a region.

Eight potential hotspots for cephalopods were examined throughout the wider Caribbean (Figure 3); the coordinates for each are provided in Supplementary Table S1. The eight sites were chosen by location in the wider Caribbean based on the species-richness study of Smith *et al.* (2002). Species numbers in hotspots were calculated using an Excel spreadsheet for comparison of the eight subareas. Rarefaction curves for the sites were created using Primer 6.2 (Clark and Gorley, 2001), for comparison of the species observed and the Chao 1 estimator.

Results

Species richness in the wider Caribbean increased with increasing latitude. The 8–10°N band had the lowest species richness,

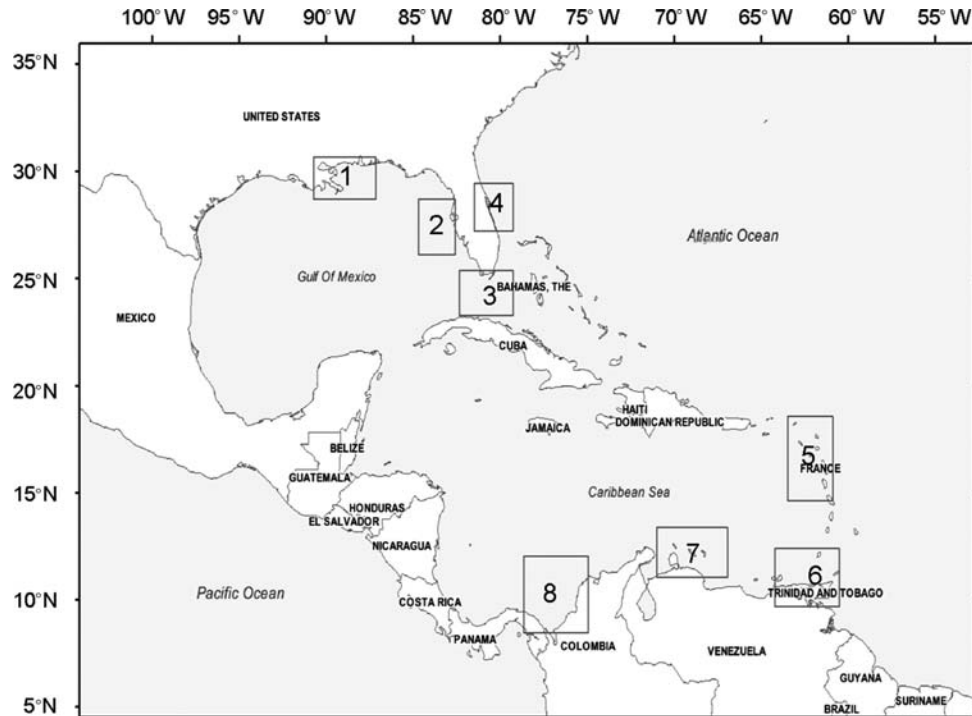


Figure 3. The eight subareas for richness and diversity comparison. Subarea 1, northern Gulf of Mexico; Subarea 2, western central Florida; Subarea 3, Straits of Florida; Subarea 4, Eastern central Florida; Subarea 5, Mid-Island Caribbean group; Subarea 6, southeastern Caribbean Sea; Subarea 7, southern central Caribbean Sea; Subarea 8, southwestern Caribbean Sea-Colombia area.

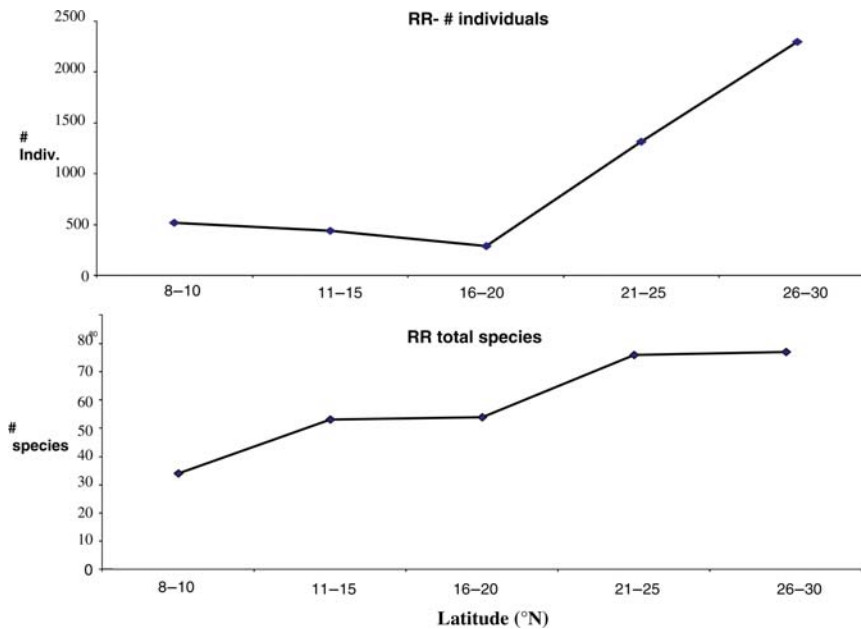


Figure 4. Comparison of (top) the total number of species and (bottom) the number of individuals per band of latitude.

34 species, gradually increasing up through the higher latitudes to the 26–30°N band, with 77 species. Figure 4 compares the number of individual cephalopods examined with the number of species found in each latitudinal band. There was an increase in species found per band, but the number of individuals varied among bands. Latitude bands 11–15 and 16–20°N showed a decrease

in individuals examined whereas species richness increased, indicating that sampling effort was not the sole factor for species richness increasing northwards. All latitude bands headed towards an asymptote in the species-observed rarefaction curves (Figure 5), but only the higher latitudes appeared to approach it. The Chao 1 estimator curve (Figure 6) represents the expected number of

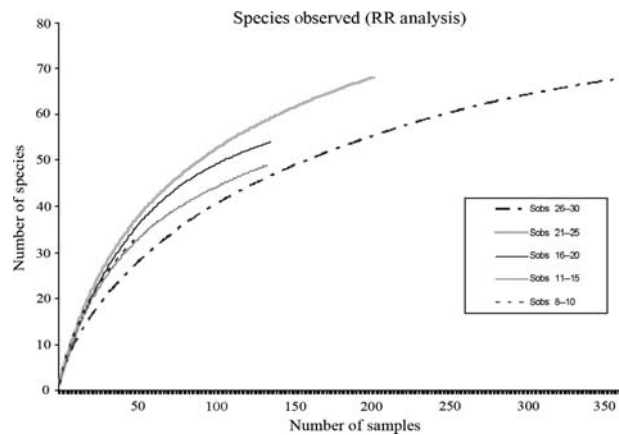


Figure 5. Rapoport rule rarefaction curves for total species observed per band of latitude.

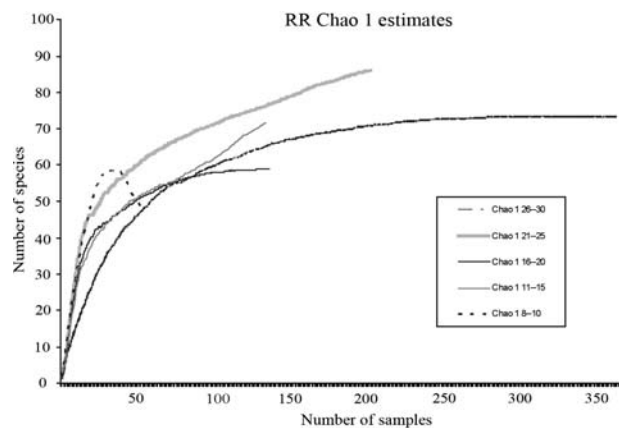


Figure 6. Rapoport rule samples. Chao 1 estimator results for the expected number of species per band of latitude.

species found in each band and shows that species richness estimates are conservative in all latitudes with respect to actual numbers of species observed (Table 1).

Table 2 compares the number of species per region in the eight hotspots. Samples represent the number of individuals within each region. Clearly, Subarea 4 (eastern central Florida) has the greatest species richness ($n = 32$), followed by Subarea 1, northern Gulf of Mexico ($n = 27$), Subarea 3 in the Straits of Florida ($n = 22$), Subarea 8 in the southwestern Caribbean Sea ($n = 20$), Subarea 2 off western central Florida ($n = 13$), Subarea 5 ($n = 11$), Subarea 6 ($n = 4$), and finally Subarea 7 ($n = 3$).

Rarefaction curves were used to determine the expected number of species per subarea as a function of organisms sampled. Figures 7 and 8 show the rarefaction and Chao 1 curves derived for each subarea. Subregion 6 was not included because so few samples were obtained there ($n = 4$). The trend-lines within each graph are similar, with differences between subareas in proximity to each other. For example, Subareas 7 and 8 are both in the lower Caribbean Sea yet show large differences in both species observed and expected species. Another difference in subarea species richness is between Subareas 2 and 4. Subarea 2, the eastern central Gulf of Mexico, has many fewer species observed and expected number of species than Subarea 4, at approximately the same latitude.

Table 1. RR species richness comparison results, showing the raw data, rarefaction, and the Chao 1 estimator for the number of species per band of latitude.

Latitude (°)	Raw data	Rarefaction	Chao 1
8–10	34	34	58.7
11–15	53	49	71
16–20	54	54	59
21–25	76	68	86.05
26–30	77	68	73.14

Table 2. Regional numbers of species and samples for hotspot regional comparison.

Location	Region	Number of species	Number of samples
Northern Gulf of Mexico	1	27	46
Western central Florida	2	13	151
Straits of Florida	3	22	32
Eastern central Florida	4	32	68
Mid-Island Group	5	11	17
Southeastern Caribbean	6	4	4
Southern central Caribbean	7	3	10
Southwestern Caribbean – Colombia	8	20	25

Discussion

RR attributes the many observations of increasing diversity with decreasing latitude to a reduction in size of species' distributional ranges as one approaches the equator. Stevens (1989) supported his claim with studies of diverse taxa including North American trees, North American marine molluscs, freshwater and coastal fish, reptiles, and amphibians.

Since that time, many scientists have studied the ecological patterns driving biological diversity. There has been much debate whether RR is a genuine rule or just an effect, because it cannot be applied successfully to so many datasets. There have been many hypotheses to explain diversity patterns (Peet, 1974; Hillebrand, 2004), and various groups of organisms have been examined to test RR. Many studies of marine groups have supported RR (Steele, 1988; Stevens, 1996; Roy *et al.*, 1998, 2000; Rex *et al.*, 2000, 2005; Macpherson, 2002), but others have failed to find a relationship (Clarke, 1992; Lamshead *et al.*, 2000; Mokievsky and Azovsky, 2002; Rosa *et al.*, 2008). Whether RR is regarded as a genuine rule or not, discussion of it as a rule has served the important function of focusing attention on the possible consequences and determinants of spatial variation in geographic range sizes (Gaston *et al.*, 1998).

There have been a few molluscan species richness studies in the Atlantic Ocean to date (Macpherson, 2003; Fortes and Absalao, 2004; Rosa *et al.*, 2008). Fortes and Absalao (2004) examined gastropods and bivalves using literature-based studies from both the Pacific and Atlantic sides of continental North and South America. After analysing 4067 species, they concluded that RR applied to these organisms on both coasts. They noted that regional features, such as the size of a biogeographic province, seemed to influence the pattern strongly. They also found support for RR when they incorporated depth into the study. Macpherson (2003) studied the variability in the size of species ranges in terms of depth and latitude for various marine taxa, including cephalopods and fish

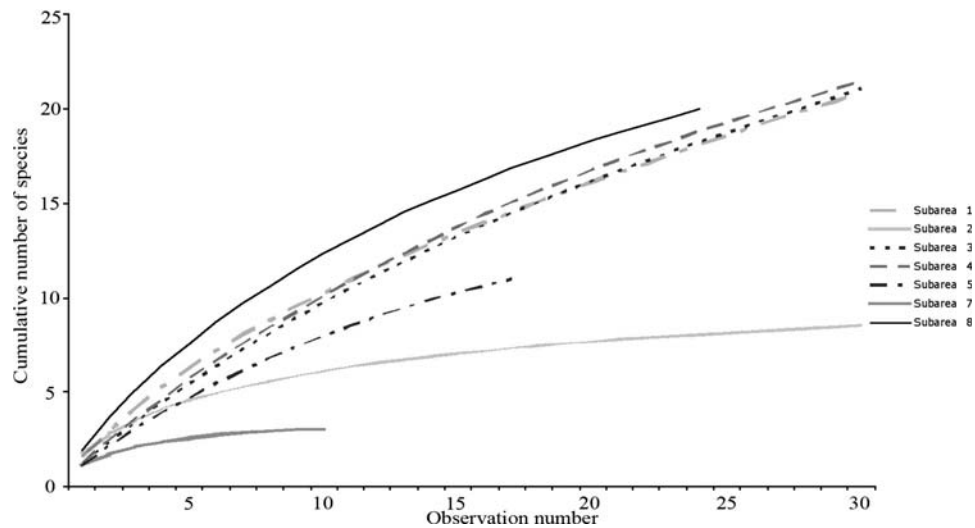


Figure 7. Rarefaction results for species observed per hotspot subarea.

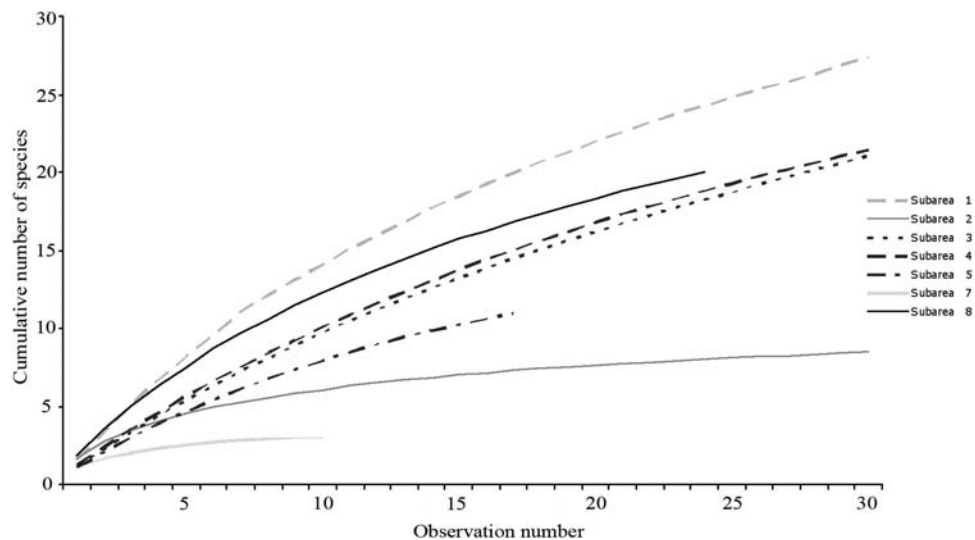


Figure 8. Chao 1 estimator comparison of hotspot subareas, in terms of the expected number of species per band of latitude.

in the Atlantic Ocean. His results showed that RR could hold true for those organisms, but could not solely be deemed responsible for latitudinal patterns in range sizes. The research of Rosa *et al.* (2008) examined cephalopod species of the coastal Atlantic Ocean using primary literature, grey literature, and online databases. Their results showed that latitudinal gradients of species richness were present along both Atlantic coasts, but were distinct from each other. When the median latitudinal ranges of western Atlantic neritic cephalopods were determined, it was evident that the size of the distributional ranges did not decline with decreasing latitude, meaning that RR may not explain the distribution patterns. Stevens (1996) proposed that RR could extend to elevation and water depth in terms of species richness. When species depths were taken into consideration for the organisms in the western Atlantic, RR was exhibited (Rosa *et al.*, 2008).

The present specimen-based study showed that cephalopods of the wider Caribbean do not exhibit the diversity patterns described originally by Stevens (1989). Within the small latitudinal range 8–30°N, cephalopods of the region increase in species richness

with increasing latitude. The small range of latitudes allowed for detailed analysis on more than 4000 specimens that fill various niches within the wider Caribbean. Many past RR studies (Sanders, 1968; Rapoport, 1982; Stevens, 1989; Fortes and Absalao, 2004) utilized large and northern latitudinal ranges, and there was both support and non-support for RR. This small-scale latitude study is another piece to complete the RR picture. The lack of accord we found with RR agrees with the finding of Rosa *et al.* (2008), although it should be noted that the lowest latitude band (8–10°N) includes just 3° of latitude and the other four bands cover 5° in each. Therefore, there may be more than the 34 species in the 8–10°N band than the present study suggests. However, even without that latitude band, the species richness trend is still obvious as latitude increases.

One of the reasons for an increase in species numbers at higher latitudes could be the convergence of the Florida Current and the North Equatorial Current in the central to northern end of the study area. The two currents converge to become the Gulf Stream and may transport cephalopods northwards. The Gulf

Stream then leaves the coast of the eastern United States at Cape Hatteras, NC, to head eventually across the Atlantic Ocean. That current has a profound influence on the distribution of shore animals in the western Atlantic (Briggs, 1995).

Another factor possibly contributing to the northward increase in species richness is the larger number of studies in the northern wider Caribbean region. Many studies have been conducted in Florida waters, which may contribute to the increased richness of cephalopods in the northern portion of the study area. The rarefaction curves in Figure 5 demonstrated a similar richness trend for all regions and support a call for more sampling in the lower latitude, because the northern two bands were close to the asymptote whereas the southern three bands were still rising. The Chao 1 estimator analysis showed differences among species richness between the bands. Note that the 8–10°N latitude band approached 60 species expected, but then decreased rapidly (Figure 6). A possible reason for that decline is that there was a very small sample size for that latitude band, with many singleton species enumerated. These two analyses suggest that increased sampling is not the sole reason for northward increases in species richness within the region.

Cephalopod biogeography

Based on the range map overlays, Smith *et al.* (2002) examined the distribution of 1172 vertebrate and invertebrate species in the western central Atlantic and concluded that the area of greatest species richness was in the waters surrounding southern Florida, the eastern Bahamas, and northern Cuba. Secondary centres of diversity were located (in descending order of richness) on the continental shelves of northern South America, central America, and in the northern Gulf of Mexico. Those patterns are apparently robust, because they are repeated in composite distributions for fish and for other invertebrates taken separately (Smith *et al.*, 2002).

Eight subareas (Figure 3) were used to compare cephalopod species richness within the wider Caribbean. Each subarea incorporated features of biogeographic significance, e.g. important current patterns or seafloor features, or exhibited potential as resource management areas. Based on the cephalopod species richness information presented here, eastern central Florida has the greatest species richness in the wider Caribbean ($n = 32$), likely because the Gulf Stream acts as a large transporter of paralarvae from southern waters. Another possible, but less likely, factor for this subarea's species richness is that it lies in an important path for seasonally migrating cephalopods (Perez and O'Dor, 1998). The representative species are listed in Supplementary Table S2.

The cephalopods of the wider Caribbean generally follow the pattern shown by Smith *et al.* (2002) in that the two subareas exhibiting the greatest richness were the same in both studies. However, Subarea 6, the southeastern Caribbean Sea, had too few samples to be included in the analysis ($n = 4$); Subarea 7, the southern central Caribbean Sea, had ten samples and was included. Smith *et al.* (2002) suggested that the southern edge of the Caribbean was the second richest in terms of species, whereas the present study does not allow a similar conclusion to be drawn. The two areas of low sampling effort (6 and 7) over 111 years of collecting indicate a need for further fieldwork in those regions.

The subarea rarefaction curves display curious trends within the wider Caribbean. It was anticipated that there would be variations in species richness between the major basins of the

Caribbean and the Gulf of Mexico. This does not appear to be the case. For example, Subareas 7 and 8 were both located in the lower Caribbean and yet showed significantly different trends in species richness (Figure 7). Another example of variation within regions can be seen between Subareas 2 and 4 in the northern sections of the region. A reason for the variation in this case could be the intensive work conducted during the Hourglass cruises of the mid-1960s by the Marine Research Laboratory of the Florida Board of Conservation, creating an artefact from sampling effort alone. Two experts identified and catalogued cephalopod shelf species which were included in the present study. Although >500 specimens were included in Subarea 2, the cephalopod species richness of the subarea ($n = 13$) was still less than that of Subareas 3 ($n = 22$) and 4 ($n = 32$). Another explanation for the increase in species richness in Subarea 4 could be the influence of water depth changes and the flow of the Gulf Stream. These two examples of variation within regions (Gulf of Mexico and Caribbean basin) exceed the variations between the northern and southern regions of the study's scope.

To summarize, there is no support for RR for cephalopods of the wider Caribbean. Hotspots are patchy, with greatest species richness along the eastern edge of Florida in the Gulf Stream. Areas of the southeastern Caribbean and the western Gulf of Mexico appear to be undersampled, at least among collections available for this study.

A problem with these observations is that there is generally no way of knowing from museum records what percentage of specimens was archived from different field projects. Museums tend to accession only what is sent to them. The principal investigator on a field project may send every specimen collected, or perhaps just vouchers of every presumed species, or just material for which they want help with identification. It is difficult to obtain every specimen from any net haul, and some may be damaged beyond recognition. Once at the museum, the curator may decide that they do not need, or do not have space for many loliginids (for example), so only a subset would be catalogued into the permanent collection. Perhaps too, only "museum-quality" specimens are retained and those in poor condition discarded. These factors vary among sets of samples and among museums and curators, so all would add a level of inaccuracy on the top of problems such as gear selectivity or other sampling biases. Although there is no perfect way to assess biodiversity, the optimum would be to sample the entire region essentially at the same time with multiple gears, then repeat the exercise over multiple seasons and multiple years and include accurate identifications of every animal collected. That, of course, would be impractical. What we have done here, therefore, is to try to develop the best inference of patterns from actual specimens that have been retained from previous fieldwork.

Marine resource conservation and management in the wider Caribbean is slowly becoming a reality as groups work towards a large marine ecosystem governance framework for the area (Fanning *et al.*, 2007). That framework is the first step in the eventual effective management of shared marine resources. Proper identification and collection of cephalopods will provide a better understanding of potential cephalopod fisheries. More than half the global cephalopod catch recorded by the FAO is not segregated into single species, significantly reducing any value the data may have for population assessment (Boyle and Boletzky, 1996). Cephalopod hotspots and diversity trends are important not only to fisheries but also to conservation groups working with

intricate foodweb assemblages and determining the importance and roles of cephalopods in the region. Studies on all aspects of cephalopod life history, diversity, biology, ecology, and capture methods would improve the world's database for these organisms.

Supplementary material

Supplementary material is available at *ICESJMS* online.

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References

- Boyle, P. R., and Boletzky, S.v. 1996. Cephalopod populations, definition, and dynamics. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 351: 985–1002.
- Briggs, J. C. 1995. *Global Biogeography*. Elsevier Science, Amsterdam. 454 pp.
- Cairns, S. 1976. Cephalopods collected in the Straits of Florida by the RV Gerda. *Bulletin of Marine Science*, 26: 233–272.
- Clark, K. R., and Gorley, R. N. 2001. *PRIMER v6: User Manual/Tutorial*. PRIMER-E, Plymouth, UK. 190 pp.
- Clarke, A. 1992. Is there a latitudinal diversity cline in the sea? *Trends in Ecology and Evolution*, 7: 286–287.
- Clarke, M. R. 1996. The role of cephalopods in the world's oceans: an introduction. *Philosophical Transactions of the Royal Society of London, Series B*, 351: 979–983.
- Díaz, J. M. 2004. First record of an octopus species of the family Tremoctopodidae (Cephalopoda: Octopoda) for the Colombian Caribbean. *Biological Investigations of Marine Coasts*, 33: 283–286.
- Díaz, J. M., Ardila, N., and Gracia, N. 2000. Calamares y pulpos (Mollusca: Cephalopoda) del Mar Caribe Colombiano. *Biota Colombiana*, 1: 195–201.
- Fanning, L., Mahon, R., McConney, P., Angulo, J., Burrows, F., Chakalall, B., Gil, D., *et al.* 2007. A large marine ecosystem governance framework. *Marine Policy*, 31: 434–443.
- Fortes, R. R., and Absalao, R. S. 2004. The applicability of Rapoport's rule to the marine molluscs of the Americas. *Journal of Biogeography*, 31: 1909–1916.
- Gaston, K. J., Blackburn, T. M., and Spicer, J. I. 1998. Rapoport's rule: time for an epitaph? *Trends in Ecology and Evolution*, 13: 70–74.
- Gotelli, N., and Colwell, R. K. 2004. Quantifying biodiversity: procedures, and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, 4: 379–391.
- Gracia, A. 2002. Cephalopods (Mollusca: Cephalopoda) of the Upper Colombian Caribbean Shelf. *Biological Investigations of Marine Coasts*, 31: 219–238.
- Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. *American Naturalist*, 163: 192–211.
- Jereb, P., and Roper, C. F. E. 2005. *Cephalopods of the World. An Annotated and Illustrated Catalogue of Cephalopod Species Known to Date*. FAO Species Catalogue for Fisheries Purposes, 1(4). FAO, Rome. 262 pp.
- Judkins, H. L. 2009. *Cephalopods of the wider Caribbean: distribution, abundance, and ecological importance*. Dissertation, College of Marine Science, University of South Florida, St Petersburg. 147 pp.
- Lambshead, P. J. D., Tietjen, J., Ferraro, T., and Jensen, P. 2000. Latitudinal diversity gradients in the deep sea with special reference to North Atlantic nematodes. *Marine Ecology Progress Series*, 194: 159–167.
- LaRoe, E. T. 1967. A contribution to the biology of the Loliginidae (Cephalopoda: Myopsida) of the tropical western Atlantic. MSc thesis, University of Miami, Coral Gables, FL.
- Lesueur, C. A. 1821. Description of several new species of cuttle-fish. *Journal of the Academy of Natural Sciences of Philadelphia*, 2: 86–101.
- Lipka, D. A. 1975. The systematics and zoogeography of cephalopods of the Gulf of Mexico. PhD thesis, Texas A&M University. 204 pp.
- Macpherson, E. 2002. Large-scale species-richness gradients in the Atlantic Ocean. *Proceedings of the Royal Society of London, Series B*, 269: 1715–1720.
- Macpherson, E. 2003. Species range size distributions for some marine taxa in the Atlantic Ocean. Effect of latitude and depth. *Biological Journal of the Linnean Society*, 80: 437–455.
- Magurran, A. E. 2004. *Measuring Biological Diversity*. Blackwell Publishing, Oxford. 256 pp.
- Mokievsky, V., and Azovsky, A. 2002. Re-evaluation of species diversity patterns of free living marine nematodes. *Marine Ecology Progress Series*, 238: 101–108.
- Nesis, K. N. 1987. *Cephalopods of the World*. TFH Publications, New Jersey. 351 pp.
- Passarella, K. C. 1990. Oceanic cephalopod assemblage in the eastern Gulf of Mexico. Department of Marine Science, University of South Florida, St Petersburg. 50 pp.
- Peet, R. K. 1974. The measurement of species diversity. *Annual Review of Ecology and Systematics*, 5: 285–307.
- Perez, J. A. A., and O'Dor, R. K. 1998. The impact of environmental gradients on the early life inshore migration of the short-finned squid, *Illex illecebrosus*. *South African Journal of Marine Science*, 20: 293–303.
- Rapoport, E. H. 1982. *Areography: Geographical Strategies of Species*, 1st English edn. Translated by B. Drausal. Pergamon, New York.
- Rex, M. A., Crame, J. A., Stuart, C. T., and Clarke, A. 2005. Large-scale biogeographic patterns in marine molluscs: a confluence of history and productivity? *Ecology*, 86: 2288–2297.
- Rex, M. A., Crame, J. A., Stuart, C. T., and Coyne, G. 2000. Latitudinal gradients of species richness in the deep-sea benthos of the North Atlantic. *Proceedings of the National Academy of Sciences of the USA*, 97: 4082–4085.
- Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*, 65: 514–527.
- Roper, C. F. E., Sweeney, M. J., and Nauen, C. E. 1984. FAO species catalogue. 3. Cephalopods of the world. An annotated and illustrated catalogue of species of interest to fisheries. FAO Fisheries Synopsis, 125(3). 277 pp.
- Rosa, R., Dierssen, H. M., Gonzalez, L., and Seibel, B. 2008. Ecological biogeography of cephalopod molluscs in the Atlantic Ocean: historical and contemporary causes of coastal diversity patterns. *Global Ecology and Biogeography*, 17: 600–610.
- Roy, K., Jablonski, D., and Valentine, J. W. 2000. Dissecting latitudinal diversity gradients: functional groups and clades of marine bivalves. *Proceedings of the Royal Society of London, Series B*, 267: 293–299.
- Roy, K., Jablonski, D., Valentine, J. W., and Rosenberg, G. 1998. Marine latitudinal diversity gradients: tests of causal hypotheses. *Proceedings of the National Academy of Sciences of the USA*, 95: 3699–3702.
- Sanders, H. L. 1968. Marine benthic diversity: a comparative study. *American Naturalist*, 102: 243–282.
- Simberloff, D. 1978. Use of rarefaction and related methods in ecology. In *Biological Data in Water Pollution Assessment: Quantitative and Statistical Analysis*, pp. 150–165. Ed. by K. L. Dickson, J. Cairns, and R. J. Livingston. American Society for Testing and Materials, Philadelphia, PA.
- Smith, M. L., Carpenter, K. E., and Waller, R. W. 2002. An introduction to the oceanography, geology, biogeography, and fisheries of the tropical and subtropical western central Atlantic. In *The*

- Living Marine Resources of the Western Central Atlantic. 1. Introduction, Molluscs, Crustaceans, Hagfishes, Sharks, Batoid Fishes, and Chimaeras, pp. 1–23. Ed. by K. E. Carpenter. FAO Species Identification Guide for Fisheries Purposes and American Society of Ichthyologists and Herpetologists, Special Publication 5. FAO, Rome. 600 pp.
- Stanley, S. (Ed). 1995. A Global Representative System of Marine Protected Areas. Volume 2, Marine Region 7: Wider Caribbean, pp. 15–42. Great Barrier Reef Marine Park Authority, The World Bank, The World Conservation Union (IUCN).
- Steele, D. H. 1988. Latitudinal variations in body size and species diversity in marine decapod crustaceans of the continental shelf. *International Review of Hydrobiology*, 73: 235–246.
- Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist*, 133: 240–256.
- Stevens, G. C. 1996. Extending Rapoport's rule to the Pacific marine fishes. *Journal of Biogeography*, 23: 149–154.
- Vecchione, M. 2002. Cephalopods. *In* The Living Marine Resources of the Western Central Atlantic. 1. Introduction, Molluscs, Crustaceans, Hagfishes, Sharks, Batoid Fishes, and Chimaeras, pp. 149–244. Ed. by K. E. Carpenter. FAO Species Identification Guide for Fisheries Purposes and American Society of Ichthyologists and Herpetologists, Special Publication 5. FAO, Rome. 600 pp.
- Vecchione, M., Mickevich, M. F., Fauchald, K., Collette, B. B., Williams, A. B., Munroe, T. A., and Young, R. E. 2000. Importance of assessing taxonomic adequacy in determining fishing effects on marine diversity. *ICES Journal of Marine Science*, 57: 677–681.
- Voss, G. L. 1954. Cephalopods of the Gulf of Mexico. *In* Gulf of Mexico, its Origin, Waters, and Marine Life, pp. 475–478. Ed. by P. S. Galtsoff. *Fishery Bulletin US*, 89.
- Voss, G. L. 1956. A review of the cephalopods of the Gulf of Mexico. *Bulletin of Marine Science of the Gulf and Caribbean*, 6: 85–178.
- Voss, G. L. 1973. The potentially commercial species of octopus and squid of Florida, the Gulf of Mexico and the Caribbean Sea. University of Miami Sea Grant Program (NOAA Sea Grant No. 04-3-158-27), Miami, FL.

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