

Species range size distributions for some marine taxa in the Atlantic Ocean. Effect of latitude and depth

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The range size distributions of 6643 species in ten different fish and invertebrate taxa dwelling in pelagic (latitudinal range sizes) and benthic (latitudinal and depth range sizes) habitats on both sides of the Atlantic Ocean (80°N–70°S) were studied. The objectives were to analyse: (1) the range size distribution patterns for the various taxa and whether they have right/left skewed or lognormal distributions; (2) the geographical species distributions, to ascertain whether the distribution ranges change with latitude (Rapoport's rule); and (3) the relationship between the depth ranges of benthic species and their maximum depth of occurrence and how depth range size distributions change with latitude. The pelagic taxa exhibited larger range sizes than did the benthic taxa, continental slope/rise species excepted. On the other hand, the boundaries between geographical provinces for both benthic taxa and pelagic taxa tended to occur in association with major oceanographic processes. The shape of the latitudinal range frequency distributions (LRFDs) of the pelagic organisms were distinctly left-skewed, and the LRFDs for most taxa were significantly different from lognormal. There was no common pattern for the distributions of the benthic organisms, which were lognormal in Cephalopoda, Stomatopoda, and Crustacea Decapoda and tended to be left-skewed and significantly different from lognormal in Pisces. The applicability of Rapoport's rule was not clearly inferable from the results, and the rule appears to be conditioned by the location of biogeographical boundaries and the endemism rate in the different biogeographical provinces. A clear increase in depth range size with maximum depth range was observable for benthic species, confirming previous studies. Species' depth range distributions displayed a discernible latitudinal pattern, right-skewed at high latitudes and left-skewed at low latitudes. The location of biogeographical boundaries, and endemism rate by biogeographical province were considered to be the factors most useful in explaining species' distribution patterns and their conformity or nonconformity to Rapoport's rule. © 2003 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2003, **80**, 437–455.

ADDITIONAL KEYWORDS: Atlantic Ocean – biogeography – geographical range – Rapoport's rule.

INTRODUCTION

Species' geographical distributions and range sizes are one of the central issues in ecology, and recent studies have shown that it is difficult to apply general rules to different groups of organisms (Brown, 1995; Brown, Stevens & Kaufman, 1996; Gaston, 1998; Gaston & Blackburn, 2000). Most studies have focused on two different aspects: (1) patterns in species' range size distributions (Gaston, 1996) and (2) the effect of latitude on species' range sizes, i.e. Rapoport's rule (Stevens, 1989).

Less attention has been paid to the first of these aspects, though various studies have revealed certain interesting general tendencies, e.g. range sizes for terrestrial taxa are usually smaller than for marine taxa, plants and insects ordinarily have smaller ranges than vertebrates, and mammalian carnivores have larger ranges than herbivores (Anderson, 1985; Pagel, May & Collie, 1991; Fenchel, 1993; Roy, Jablonski & Valentine, 1994; Ruggiero, 1994; Brown *et al.*, 1996; Gaston & Blackburn, 1996, 2000; Gaston, 1996, 1998; Hecnar, 1999; Gaston & He, 2002). These studies have shown that for a given taxon most species will have small ranges, yielding distinctly right-skewed distributions. On log transformation the ranges tend to be lognormal, although sometimes they can be moderately left-

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skewed (Blackburn & Gaston, 1996; Brown *et al.*, 1996; Gaston, 1996, 1998; Williamson & Gaston, 1999). Despite the interest such studies hold out for inventories of flora and fauna and the repercussions they may have on conservation strategies (Roberts *et al.*, 2002), little research has covered both a broad range of species groups and a wide geographical area (Gaston, 1996, 1998). This has made it difficult to establish the extent to which these patterns are in fact broadly applicable and at the same time it has prevented elucidation of the regulatory mechanisms at work.

The second of these aspects, Rapoport's rule, has been studied for many different groups since Stevens (1989) first discerned the tendency for specific range size to increase with latitude (see Gaston, Blackburn & Spicer, 1998; Rohde, 1999; Gaston & Blackburn, 2000; for an extensive review of the groups that have been studied). Rapoport's rule (Stevens, 1989), or the Rapoport effect (Ruggiero & Lawton, 1998), has been attributed to the broader climatic fluctuations at higher latitudes, which require species dwelling in those areas to develop greater tolerance, thus allowing them to inhabit a wider range of climatic conditions than species from lower latitudes, i.e. the seasonal variability hypothesis (see the review by Gaston & Blackburn, 2000). This trend has been studied in both terrestrial (Rapoport, 1982; Stevens, 1989; Letcher *et al.*, 1994; Ruggiero, 1994; Smith, May & Harvey, 1994; Mourelle & Ezcurra, 1997; Ruggiero & Lawton, 1998; Ruggiero, Lawton & Blackburn, 1998; Hecnar, 1999; Harcourt, 2000) and marine (Rohde, Heap & Heap, 1993; Macpherson & Duarte, 1994; Roy *et al.*, 1994; Stevens, 1996) organisms. Broadly speaking, this postulated latitudinal gradient has been observed not to be general and on the whole not to exist on a broad scale, though it may exist on a local or regional scale (Rohde & Heap, 1996; Gaston *et al.*, 1998; Rohde, 1999; Gaston & Blackburn, 2000). Furthermore, certain workers have shown that latitudinal species ranges depend not so much on latitude as on the spatial distribution of the principal biogeographical barriers (Roy *et al.*, 1994; Gaston, 1998; but see Colwell & Hurt, 1994). A second feature of the Rapoport effect, based on the seasonal variability hypothesis, suggests that mean latitudinal range sizes increase with altitude, again as a consequence of the greater climatic tolerance of the species dwelling at higher altitudes (Stevens, 1992). This pattern has been examined in terrestrial species, but the number of studies has been too few to corroborate the pattern as generally applicable (Stevens, 1992; Ruggiero & Lawton, 1998). Similarly, based on seasonal surface temperature variations with depth and latitude, Stevens (1996) proposed a third extension to Rapoport's rule (Rapoport's depth rule). Depth range size distributions have been considered for certain taxa, and the tendency for

depth range to increase with depth of occurrence has been observed in numerous studies (e.g. Ekman, 1953; Vinogradova, 1959; Hansen, 1975; Sanders, 1979; Pineda, 1993; Macpherson & Duarte, 1994; Stevens, 1996; Smith & Brown, 2002).

Most studies dealing with the above-mentioned aspects have been carried out in terrestrial habitats on a limited number of taxa and have rarely covered the entire distribution ranges of the different species (Gaston, 1996). Although such work has given rise to interesting papers (see the excellent review by Gaston & Blackburn, 2000), the predominance of studies concerning terrestrial species means that both the patterns described and the underlying mechanisms that may explain them have been based on the features and factors intrinsic to these ecosystems. In contrast, the characteristics of marine organisms are quite different from those of terrestrial organisms, e.g. a predominantly pelagic larval stage, a greater capacity for dispersal and less pronounced biogeographical divisions (Margalef, 1974; Rapoport, 1994; Gray, 2001), all of which may affect their distribution patterns.

In this study the distributions of 6643 species belonging to ten marine taxa have been considered. The taxa were Hydromedusae, Siphonophorae, Cephalopoda, Euphausiacea, Stomatopoda, Crustacea Decapoda, Chaetognatha, Appendicularia, Salpida, and Pisces covering the entire Atlantic Ocean (80°N–70°S), including both the western and eastern sides as well as the central oceanic zone. Some of the groups considered comprise few species, but they have nonetheless been included in the study on the understanding that analysing the distribution patterns of organisms differing in biology and in phylogeny may help identify the mechanisms underlying those patterns. Consideration of diverse, taxonomically distant groups with very different larval and adult dispersal capabilities, inhabiting regions from the coastal zone down to the abyssal zone, and being both pelagic and benthic in habit, may contribute to a more complete analysis of existing patterns and regulatory mechanisms. Using this broad number of taxa and species, this study has analysed: (1) the range size distribution patterns for the various taxa and whether they have lognormal distributions; (2) the geographical species distributions, to ascertain whether the distribution ranges change with latitude; and (3) the relationship between the depth ranges of benthic species and their maximum depth of occurrence and how depth range size distributions change with latitude.

MATERIAL AND METHODS

DATA SELECTION

The ten taxa considered in this study were selected because there exists an acceptable level of knowledge

of their taxonomy and distribution in the Atlantic Ocean. Although new species are still being described in some of these taxa, it has been assumed that new descriptions or citations will not significantly change the patterns described here. The species database has been compiled by means of an exhaustive search of the primary literature. The main data sources for each taxa were the following (see also the references cited in each work for a more complete list of references): Hydromedusae (Pages, Gili & Bouillon, 1992; Bouillon, 1999), Siphonophorae (Pages & Gili, 1992; Pugh, 1999), Cephalopoda (Villanueva & Sanchez, 1993; Voss *et al.*, 1998; Nesis, 1999), Euphausiacea (Gibbons, Spiridonov & Tarling, 1999), Stomatopoda (Manning, 1969, 1977), Crustacea Decapoda (Macpherson, 1991; Udekem d'Acoz, 1999; Boschi, 2000), Chaetognatha (Casanova, 1999), Appendicularia (Esnal, 1999), Salpida (Esnal & Daponte, 1999) and Pisces (Randall, 1983; Menezes & Figueiredo, 1985; Whitehead *et al.*, 1986; Böhlke, 1989; Gon & Heemstra, 1990; Quero *et al.*, 1990). Furthermore, an additional and exhaustive search was carried out in journals usually including papers on taxonomy and biogeography of Atlantic species (see Macpherson, 2002 for a list of the journals).

The following taxonomic groups were considered: Hydromedusae (294 species), Siphonophorae (107), Cephalopoda (243), Euphausiacea (41), Stomatopoda (98), Crustacea Decapoda (1979), Chaetognatha (41), Appendicularia (60), Salpida (31), and Pisces (3749). The Hydromedusae were broken down into two subgroups (1) a holoplanktonic group, 64 species that are pelagic dwelling in all their stages, and (2) a meroplanktonic group, 230 species with a benthic polyp stage, all other stages being pelagic.

Species cited fewer than five times, species introduced into the Mediterranean through the Suez Canal, and species reported from the Cape Town and Tierra del Fuego areas only, which are presumably originally from the Indian and Pacific oceans, respectively, were excluded from the analysis. Species recorded in the water column, usually offshore of the continental shelf, were considered pelagic species. Neritic species were included in the benthic group. Most pelagic species occur offshore of the shelf break on both sides of the Atlantic and in oceanic waters, hence all pelagic species were considered together. Latitudinal analysis of large depth ranges were considered for the most numerous benthic taxa (Crustacea Decapoda and Pisces), using the categories: coastal (0–100 m), continental shelf/continental slope (100–1000 m, hereafter shelf/slope), and continental slope/continental rise (>1000 m, hereafter slope/rise) (see Lincoln, Boxshall & Clark, 1998). Data sets for benthic species were compiled separately for the two sides of the Atlantic and for the three depth provinces.

Each species was included in only one depth province based on its average depth of occurrence.

The latitudinal range for each species was calculated as the difference between the northernmost and southernmost latitude of its distribution between 80°N and 70°S latitude. The minimum and maximum reported depths were used to establish the depth range for each species.

DEFINITION OF BIOGEOGRAPHICAL PROVINCES

The procedure used by Roy *et al.* (1994) was employed to determine the boundaries of the different biogeographical provinces for each of the different taxa, by calculating the ratio, expressed as a percentage, of species whose distribution endpoints fell within any given 5° bin to the total number of species present at that latitude (see also Valentine, 1966). In order to avoid confusion, the designation of biogeographical provinces mainly followed Longhurst *et al.* (1995) and Longhurst (1998) although, in some cases, the boundaries between provinces were not exactly the same. Furthermore, in pelagic taxa, where provinces were larger than those showed by these authors, the names of the provinces were more general.

LATITUDINAL RANGE FREQUENCY DISTRIBUTIONS (LRFDS)

The shape of the latitudinal range distributions was analysed using the value of the skew of the species range distributions. Skewness is the g_1 statistic, defined as the third central moment divided by the cube of the standard deviation of the distribution. Values different from lognormal were measured using the test in Sokal & Rohlf (1995). Skewness was calculated for the set of species in each taxon over the entire Atlantic Ocean (pelagic species) and for both sides of the Atlantic (benthic species), as well as for each biogeographical province. The differences between the mean range sizes for the different taxa considered were examined using ANOVA, values being normalized after log transformation, with an unequal N HSD comparison being used to analyse the differences.

EFFECT OF LATITUDE ON GEOGRAPHICAL RANGE SIZE

To study the relationship between range size and latitude, the area considered is ordinarily divided into latitudinal bins, the mean distribution ranges of the species present in each bin are then calculated, and latitude is regressed on the mean range in each bin (Stevens, 1989). However, this relationship is difficult to test using parametric regressions because of the

spatial autocorrelation of the data, given that a species will be present in several bins. To get around this problem, some workers have used the midpoint method (Rohde *et al.*, 1993), which takes the midpoint of each species' latitudinal range as a single value, thus yielding a set of independent data points. However, this method assumes that species endpoints are distributed evenly in space, which is not altogether true when large regions are considered, as in this study. Over broad areas (e.g. an ocean) there are usually several distinct biogeographical boundaries separating different provinces (Valentine, 1966; Margalef, 1974) where the endpoints of the distributions of many species tend to converge, which may give rise to artefactual patterns (e.g. Roy *et al.*, 1994, Roy, Jablonski & Martien, 2000).

To obviate these potential problems, the present study used two different methods for its analysis of the effect of latitude on geographical range size. First, pairwise comparison of the LRFDs among the different biogeographical provinces existing in the Atlantic Ocean (Roy *et al.*, 1994, 2000). The differences in the shapes of the LRFDs and their mean values were assessed by the non-parametric Mann–Whitney *U*- and the Kolmogorov–Smirnov tests. The presence of the Rapoport effect would mean that the ranges of the latitudinal distributions would increase from the tropical provinces outwards towards the poles. These comparisons were only performed between adjacent provinces where the province contained at least ten species from each of the taxa considered. Second, a method similar to the method of Pagel *et al.* (1991) (see also Pineda, 1993) was used to analyse the relationship between the latitude furthest from the equator (north or south) in each species' latitudinal distribution and its latitudinal range. A positive relationship means that species whose distributions reach the highest latitudes also have the largest latitudinal ranges.

RELATIONSHIP BETWEEN LATITUDE, DEPTH OF OCCURRENCE AND VERTICAL RANGE

This relationship was considered only for those taxa that included benthic species (Crustacea Decapoda, Stomatopoda, Cephalopoda, and Pisces). The following analysis was performed: (1) the relationship between depth range size and maximum depth of occurrence was calculated, with a positive relationship indicating that species that attain the deepest depths also had the broadest depth ranges; (2) the skewness of the depth distributions of the benthic taxa in each biogeographical province was calculated in order to establish whether a pattern along the lines of the one put forward by Stevens (1996) was observable, i.e. a decreasing proportion of small range sizes as latitude

increased; (3) since the depth zonation of species changes with latitude (Stevens, 1996), the same procedure used to determine the biogeographical provinces (see above) was applied, calculating the ratio, expressed as a percentage, of species that had a distribution endpoint falling in each 100 m depth bin to the total number of species present at that bin. For the sake of simplicity, depth zonation was calculated separately for each biogeographical province on each side of the Atlantic (see above). Species that inhabit more than one biogeographical province may have different depth ranges, and some species have a deeper range at high latitudes than at low latitudes (Ekman, 1953). For that reason, the depth range for each biogeographical province published in the literature was used separately.

RESULTS

BIOGEOGRAPHICAL PROVINCES

Pelagic taxa exhibited two distinct biogeographical boundaries in the Atlantic, one at around 50°N and another at around 45°S (Fig. 1). The percentage of species with endpoints falling in between these two boundaries was very low, suggesting the presence of a single large biogeographical province between these two latitudes. North of 50°N there was another boundary, between 60°N and 65°N, and similarly another boundary south of 45°S, between 60°S and 65°S. These boundaries were observed for all the taxa considered, with small shifts in certain cases. Accordingly, the following provinces would appear to exist: Arctic (80°N–65°N), northern Atlantic (65°N–50°N), central Atlantic (50°N–45°S), southern Atlantic (45°S–60°S), and Antarctic (60°S to the South Pole).

For the benthic species, the percentage of endpoints falling in each 5° latitudinal bin followed quite different patterns on each side of the Atlantic. In the eastern Atlantic distinct boundaries were observed at around 65°N, 50°N, 20°N, and 15°S (Fig. 2). This pattern held for the coastal species and shelf/slope species in the different taxa but did not hold for the slope/rise species (>1000 m), for which the percentage of species with endpoints per latitudinal bin was very low over the entire eastern Atlantic, which suggests that there are no clear boundaries in the slope/rise domain. Nevertheless, an increase in the percentage of endpoints was observable around 65°N. This pattern was common to all the taxa analysed. The analysis yielded the following biogeographical provinces for the coastal and shelf/slope species in the eastern Atlantic: Atlantic Subarctic (SARC) (80°N–65°N), North-east Atlantic Continental Shelf (NECS) (65°N–50°N), Canary Current Coastal (CNRY, including the Mediterranean) (50°N–20°N), Guinea Current Coastal (GUIN)

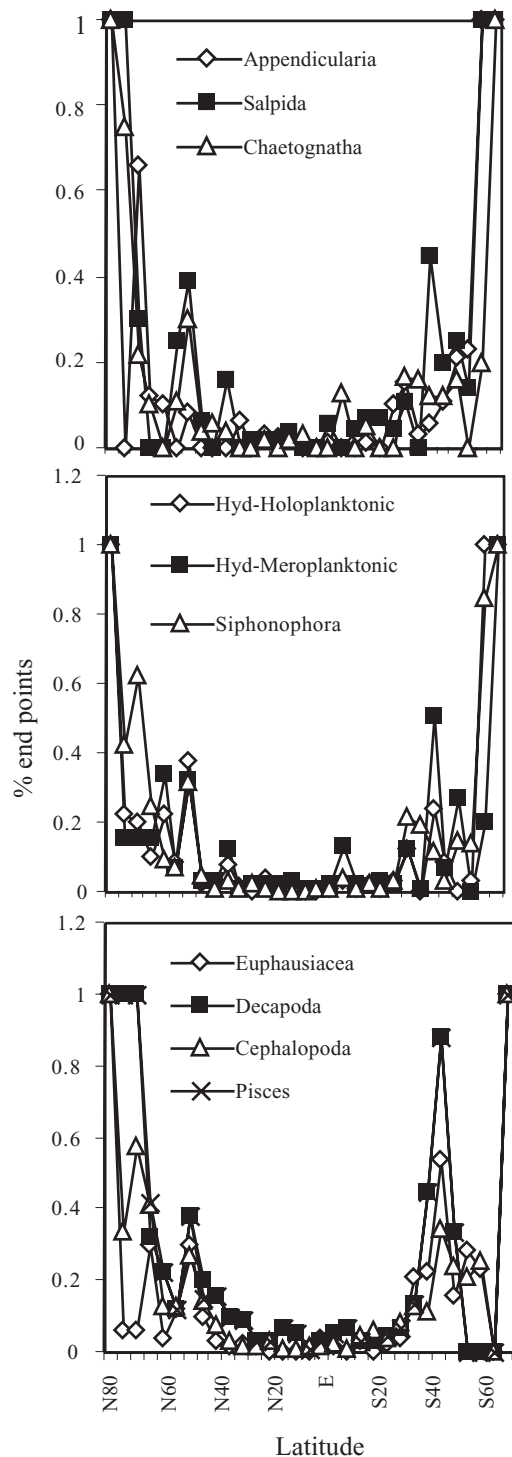


Figure 1. Latitudinal distribution of the range endpoints of pelagic taxa on the Atlantic Ocean, binned by five degrees of latitude. Each point represents the ratio, as a percentage, of species whose distribution endpoints fell within any given 5° bin to the total number of species present at that bin.

20°N–15°S and Benguela Current Coastal (BENG) 15°S–35°S (see also Longhurst *et al.* (1995) and Longhurst (1998)).

In the western Atlantic the following provinces were observed: Atlantic Arctic (ARCT) (north of 55°N), Northwest Atlantic Continental Shelf (NWCS) (55°N–35°N), Caribbean (CARB) (35°N–10°N), Guiana Current Coastal (GUIA) 10°N–25°S, Brazil Current Coastal (BRAZ, including the South-west Atlantic Continental Shelf) (25°S–55°S) and Antarctic (ANTA) (55°S–70°S) (see also Longhurst *et al.* (1995) and Longhurst (1998)). The boundaries between provinces were observed in the various taxa and in both the coastal and shelf/slope species. However, as in the eastern Atlantic, there were no clear boundaries in the slope/rise domain, with only an increase in the percentage of endpoints being observed around 50°N and 55°S (Fig. 2).

RANGE SIZE FREQUENCY DISTRIBUTIONS.

EFFECT OF LATITUDE

The ANOVA results showed that on the whole latitudinal ranges were larger for the pelagic taxa than for the benthic taxa ($F = 10.83$, $P < 0.0001$) (Table 1). The posthoc tests (unequal N HSD) showed that of the pelagic groups, the meroplanktonic Hydromedusae had the smallest ranges, which were significantly smaller than those in the other taxa (Table 2). Very few significant differences were found between benthic taxa except for slope/rise Decapoda and Pisces, which had broader ranges than most of the other groups in both the eastern and the western Atlantic (Tables 1,2). Certain pelagic species covered over 90% of the latitudinal range considered, e.g. *Dimophyes arctica* (Siphonophorae), *Modeeria rotunda* (Hydromedusae), *Sagitta maxima* (Chaetognatha), but among the benthic species only the slope/rise species attained similar ranges, e.g. *Spectrunculus grandis* (Pisces). Species with very small distributions were present in nearly all the taxa considered, with ranges occupying less than 3% of the available latitudinal range. In particular certain endemic occurrences were limited to an isolated presence in a single submarine cave, e.g. *Munidopsis polymorpha* from Lanzarote in the Canary Islands, or in a very few caves, e.g. *Somersiella sterreri*, *Typhlatya iliffei* (Crustacea Decapoda) from Bermuda or the Ascension Islands (Iliffe, Hart & Manning, 1983).

The shape of the latitudinal range frequency distributions (LRFDs) has shown the distributions of pelagic organisms to be clearly left-skewed, in most groups significantly different from lognormal after log transformation of the values (Table 1, Fig. 3). The distributions for the different groups of benthic organisms did not exhibit a single overall pattern.

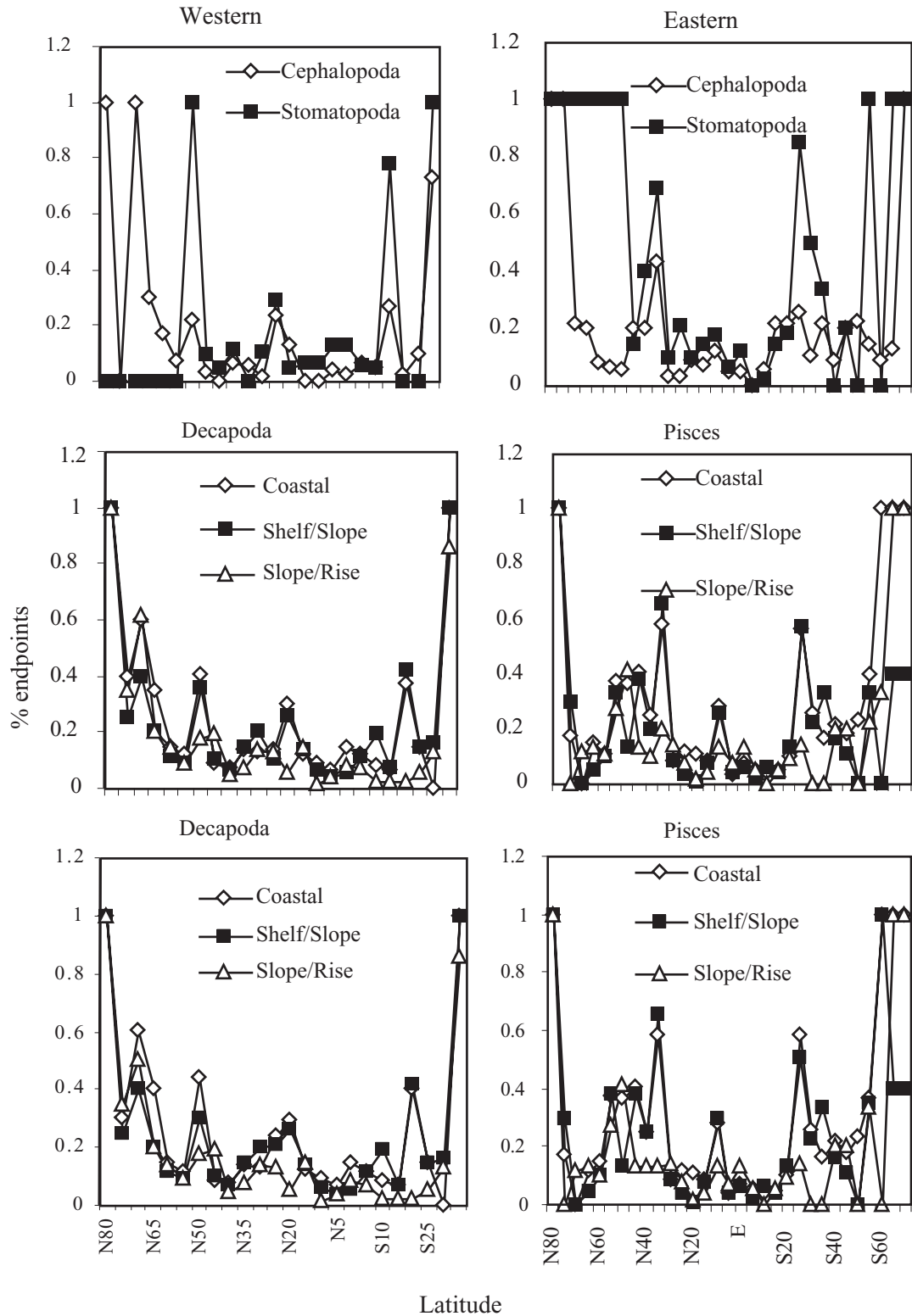


Figure 2. Latitudinal distribution of the range endpoints of benthic taxa in the western and eastern Atlantic Ocean, binned by five degrees of latitude. Each point represents the ratio, as a percentage, of species whose distribution endpoints fell within any given 5° bin to the total number of species present at that bin.

Table 1. Mean range sizes, in degrees of latitude (standard deviation, SD, in parentheses) and values of skew of the distribution of latitudinal range sizes (untransformed and log₁₀ transformed) for each taxon). *N* = number of species. E = eastern Atlantic, W = western Atlantic (skew different from log normal distribution, **P* < 0.05, ***P* < 0.01, ****P* < 0.001, NS = non-significant)

		<i>N</i>	Mean Range Size (SD)	Range Size Skewness	log ₁₀ Range Size Skewness
PELAGIC GROUP					
Hydromedusae					
		64	73.6 (42.1)	-0.21	-1.01**
		230	50.9 (41.3)	0.41	-0.43 ^{NS}
Siphonophorae					
		107	81.1 (36.3)	-0.64	-1.88***
Chaetognatha					
		41	73.9 (41.9)	0.13	-0.68 ^{NS}
Appendicularia					
		60	83.5 (39.3)	0.66	-1.66***
Salpida					
		31	64.3 (31.3)	-0.34	-1.58***
Cephalopoda					
		132	62.9 (31.3)	-0.12	-1.10***
Euphausiacea					
		41	47.8 (16.0)	-0.19	-0.76*
Crustacea Decapoda					
		105	54.7 (25.3)	-0.19	-0.98***
Pisces					
		465	67.7 (30.6)	-0.35	-1.26***
BENTHIC GROUP					
Cephalopoda					
	(E)	56	37.5 (26.5)	0.98	-0.21 ^{NS}
	(W)	55	30.3 (22.2)	1.08	-0.10 ^{NS}
Stomatopoda					
	(E)	29	26.8 (15.5)	0.60	-0.47 ^{NS}
	(W)	69	22.7 (18.5)	0.87	-0.03 ^{NS}
Crustacea Decapoda					
	(E)	432	24.1 (15.6)	1.04	-0.37 ^{NS}
	(E)	292	29.9 (18.2)	1.01	-0.53 ^{NS}
	(E)	78	38.5 (26.2)	0.83	-0.32 ^{NS}
	(W)	713	28.3 (21.2)	0.67	-0.64 ^{NS}
	(W)	320	30.4 (19.8)	0.78	-0.55 ^{NS}
	(W)	39	38.2 (26.4)	1.15	-0.29 ^{NS}
Pisces					
	(E)	728	26.8 (22.4)	1.03	-1.19***
	(E)	424	34.8 (26.9)	0.83	-1.34***
	(E)	167	53.9 (36.8)	0.69	-1.62***
	(W)	1220	30.2 (21.9)	0.78	-0.26 ^{NS}
	(W)	586	32.9 (21.5)	1.26	-1.16***
	(W)	159	54.8 (34.4)	0.15	-1.07***

Cephalopoda, Stomatopoda, and Crustacea Decapoda had distinctly right-skewed distributions that were lognormal on being log transformed. In contrast, the distribution for Pisces was slightly right-skewed but after log transformation was clearly left-skewed and significantly different from lognormal. These trends were also observable for the individual biogeographical provinces in the skewness analysis, with around 75% of the pelagic taxa having a left-skewed distribution significantly different from lognormal, compared with only 50% of the benthic taxa (Tables 3–5). In contrast, Pisces in the Antarctic province had LRFDs that were clearly right-skewed and significantly different from lognormal.

Comparison of the LRFDs for adjacent biogeographical provinces for each of the taxa considered did not reveal any common pattern (Tables 3–5). For the pelagic Chaetognatha, holoplanktonic Hydromedusae, Siphonophorae, Appendicularia, Salpida, and Pisces the mean of the LRFD in the Central Atlantic Province was less than the means for the Northern Atlantic and/or Southern Atlantic provinces (Mann–Whitney *U*-test). The differences were not significant for the meroplanktonic Hydromedusae, Cephalopoda, Euphausiacea, and Crustacea Decapoda. LRFD shape for the Arctic and Antarctic provinces differed significantly from the Northern and Southern Atlantic provinces, respectively, only for Pisces (Antarctic–Southern

Table 2. Probability values from the ANOVA (HSD post hoc test). Pelagic taxa along the Atlantic and benthic taxa from eastern (upper matrix) and western Atlantic (lower matrix) are compared separately. NS = non-significant.

PELAGIC

	Hyd. Hol.	Hyd. Mer	Siphon.	Chaet.	Apped.	Salpida	Cephal.	Euph.	Decap.	Pisces
Hydromedusae	1									
Holoplanktonic										
Hydromedusae	0.007	1								
Meroplanktonic										
Siphonophorae	NS	<0.0001	1							
Chaetognatha	NS	0.02	NS	1						
Appendicularia	NS	<0.0001	NS	NS	1					
Salpida	NS	NS	NS	NS	NS	1				
Cephalopoda	NS	NS	0.0001	NS	NS	NS	1			
Euphausiacea	NS	NS	NS	NS	NS	NS	NS	1		
Decapoda	NS	0.03	0.05	NS	NS	NS	NS	NS	1	
Pisces	NS	NS	NS	NS	NS	NS	NS	NS	NS	1

BENTHIC

(Upper half: eastern Atlantic. Lower half: western Atlantic)

	Cephal.	Stomat	D. Lit.	D. Shelf	D. Abys.	P. Lit.	P. Shelf	P. Abys.
Cephalopoda	1	NS	NS	NS	NS	NS	NS	NS
Stomatopoda	NS	1	NS	NS	NS	NS	NS	NS
Crustacea Decapoda (Coastal)	0.001	NS	1	NS	NS	0.001	NS	0.03
Crustacea Decapoda (Shelf/Slope)	NS	NS	0.001	1	NS	NS	NS	NS
Crustacea Decapoda (Slope/Rise)	NS	NS	0.002	NS	1	0.006	NS	NS
Pisces (Coastal)	NS	NS	0.001	NS	NS	1	0.001	0.001
Pisces (Shelf/Slope)	NS	NS	0.001	0.04	NS	NS	1	0.001
Pisces (Slope/Rise)	NS	0.001	0.001	0.001	NS	0.001	0.01	1

Atlantic). The differences between the mean values for the distributions also affected the distribution shapes (Kolmogorov–Smirnov test). The endemism rates in the biogeographical provinces also displayed certain patterns. The highest endemism rates for the pelagic taxa were normally present in the largest province (Central Atlantic), though there were some exceptions (i.e. Euphausiacea in the Antarctic province). For the benthic taxa, the highest endemism rate usually occurred in the Caribbean province (western Atlantic) and the Canary Current Coastal (that included the Mediterranean Sea) and Guinea Current Coastal provinces (eastern Atlantic). However, the Arctic and Antarctic provinces sometimes had still higher endemism rates (Table 3).

Pairwise comparison of the LRFDs for the benthic taxa revealed no significant differences between provinces for Cephalopoda and Stomatopoda in either the eastern or the western Atlantic (Tables 4, 5). No common pattern was observable for Crustacea Decapoda or Pisces. The mean of the LRFD for the province located at the Equator

(Guinean province) in the eastern Atlantic tended to be lower than the means for the adjacent provinces, but there were several exceptions (e.g. Benguelan vs. Guinean provinces for coastal Pisces), and very occasionally the difference with respect to both adjacent provinces was significant. There was no increase in the means of the distributions in the northernmost provinces (Atlantic Subarctic to Canary Current Coastal) with latitude, and only the mean of the distribution of coastal Decapoda was higher in the Canary Current Coastal province than in the north-east Atlantic Continental Shelf province. In the rest of the pairwise comparisons either there were no significant differences or the mean range size was lower in the more northerly province than in the more southerly province. In the western Atlantic mean range size in the most Equatorial province (Guiana Current Coastal) was higher than in the remaining provinces. As in the eastern Atlantic, no significant increase in mean range size was observed in the direction of the poles, except for continental shelf/slope Pisces (Caribbean vs. north-west Atlantic Con-

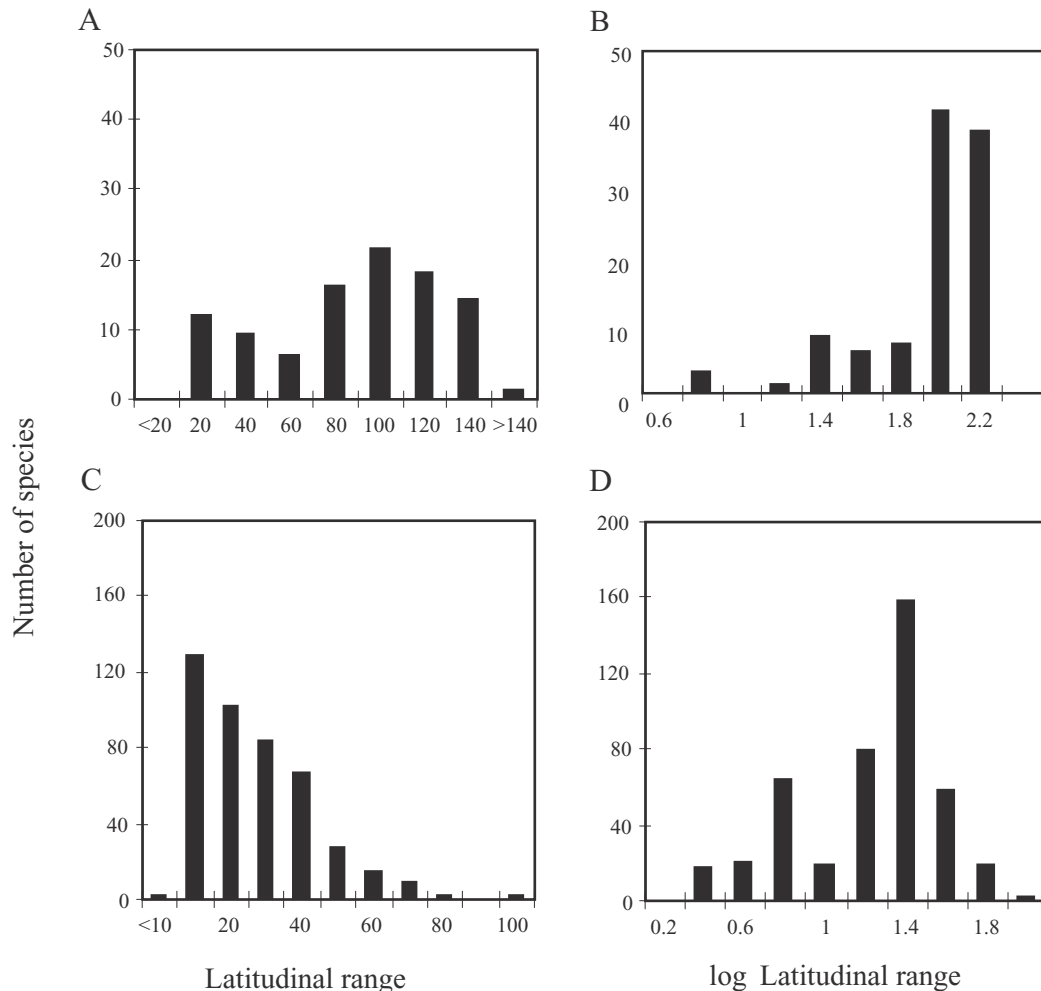


Figure 3. Frequency distributions of latitudinal range sizes for pelagic Siphonophora (A = untransformed data, B = \log_{10} transformed data) along the Atlantic Ocean and for benthic coastal Decapoda (C = untransformed data, D = \log_{10} transformed data) along the eastern Atlantic. Range in degrees of latitude.

tinental Shelf), and in some cases the mean value for the province closer to the pole was lower than the value for the province that was lower in latitude (Pisces in the Antarctic province vs. the Brazil Current Coastal province) (Tables 4, 5).

Relating the latitudinal range size for each species and the distribution endpoint located closest to the poles, significant correlations were recorded for most of the pelagic taxa (except Cephalopoda and Euphausiacea), although only a very minor proportion of the variance was explained (Table 6, Fig. 4). Of the benthic taxa, the relationship was not significant for any of the Cephalopoda and was significant for Stomatopoda only in the eastern Atlantic, while for Crustacea Decapoda and Pisces the relationship was significant for the coastal and shelf/slope provinces on both sides of the Atlantic, but not for the slope/rise species (Table 6, Fig. 4).

DEPTH OF OCCURRENCE AND VERTICAL RANGE RELATIONSHIP BY LATITUDE

The species that attained the deepest depths also had the broadest depth ranges. The relationship was highly significant for all benthic groups (Table 7).

The depth distribution ranges by biogeographical province exhibited a clear latitudinal pattern. The distributions were clearly right-skewed in the lower-latitude provinces, even after log transformation. In the provinces near the poles, the distributions were clearly left-skewed and not lognormal when log transformed (Table 8).

The boundaries for the different depth provinces changed clearly with latitude. In the biogeographical provinces nearest the poles there was hardly any zonation, with very few species having their upper or lower limits in each 100 m bin. Zonation was observed

Table 3. Mean range size (standard deviation, SD, in parentheses) and skewness of the distributions by biogeographical provinces and pairwise comparisons (Mann–Whitney *U*-test and Kolmogorov–Smirnov test) among provinces in pelagic taxa. Only contiguous provinces are considered in pairwise comparisons, and provinces with less than ten species are not analysed (level of significance, $P < 0.05$). *N* = number of species and number of endemism (in parentheses) by province. Skewness is obtained from \log_{10} transformed measures of range size (* <0.05 , ** <0.01 , *** <0.001 , NS = non-significant)

Group		Arctic (AR) 80°N–65°N	Northern (N) 65°N–50°N	Central (C) 50°N–45°S	Southern (S) 45°S–60°S	Antarctic (AN) 60°S–70°S	Mann– Whitney	Kolmogorov– Smirnov
Hydromedusae								
Holoplanktonic	<i>N</i>	9	26	48 (29)	20	15		
	Mean (SD)	90.0 (61.1)	104.4 (31.8)	92.2 (30.4)	102.5 (40.9)	99.8 (45.8)	N > C	all NS
	Skewness		–3.17***	–2.35***	–1.67**	–1.34**		
Meroplanktonic	<i>N</i>	44 (4)	93 (9)	128 (91)	30 (2)	11		
	Mean (SD)	37.1 (45.7)	79.7 (40.5)	79.7 (33.3)	70.7 (45.1)	90.5 (44.3)	all NS	C-S
	Skewness	0.93*	–1.34***	–1.85***	–0.22 ^{NS}	–0.52 ^{NS}		
Siphonophorae	<i>N</i>	5	46	102 (40)	84 (1)	19 (2)		
	Mean (SD)	81.1 (36.3)	105.2 (25.3)	84.6 (33.5)	88.5 (35.0)	92.8 (50.9)	N > C	N-C
	Skewness		–2.56***	–1.83***	–2.22***	–0.83 ^{NS}		
Chaetognatha	<i>N</i>	7	12	41 (27)	14	8		
	Mean (SD)	120.0 (42.2)	113.8 (41.3)	73.9 (41.9)	116.8 (30.9)	133.0 (10.0)	N, S > C	N-C, C-S
	Skewness		–2.60**	–0.80*	–0.88 ^{NS}			
Appendicularia	<i>N</i>	6 (1)	12	58 (12)	16	10 (2)		
	Mean (SD)	70.5 (50.1)	70.5 (47.8)	84.3 (38.3)	97.9 (45.9)	69.3 (58.0)	C < S	N-C, C-S
	Skewness		–0.83 ^{NS}	–1.35***	–2.20**			
Salpida	<i>N</i>	–	4	29	16	3 (1)		
	Mean (SD)	–	104.5 (11.2)	68.2 (28.2)	76.1 (29.5)	22.7 (15.4)	C > S	C-S
	Skewness			–1.37**	–1.31*			
Cephalopoda	<i>N</i>	4 (2)	11	95 (65)	32 (1)	9 (2)		
	Mean (SD)	40.0 (34.2)	73.9 (38.9)	76.8 (23.2)	65.8 (42.5)	24.9 (7.8)	all NS	C-S
	Skewness		–2.32**	–0.93***	0.10 ^{NS}			
Euphausiacea	<i>N</i>	7	22 (1)	51 (34)	32	5 (4)		
	Mean (SD)	79.3 (41.2)	91.8 (28.3)	72.2 (25.9)	68.9 (35.5)	13.0 (5.7)	all NS	all NS
	Skewness		–1.65**	–1.51***	–0.86*			
Decapoda	<i>N</i>	4	14 (1)	85 (81)	15 (1)	1		
	Mean (SD)	56.3 (42.7)	62.8 (34.1)	60.2 (23.1)	72.3 (25.5)	20.0	all NS	all NS
	Skewness		–0.76 ^{NS}	–1.21***	–1.99**			
Pisces	<i>N</i>	26	55 (1)	451 (339)	135	12		
	Mean (SD)	103.4 (34.6)	98.1 (33.5)	67.7 (30.6)	96.0 (18.9)	121.8 (17.5)	N > C, S < AN	N-C, C-S, S-AN
	Skewness	–1.50**	–1.71***	–1.66***	–0.62**	–0.60 ^{NS}		

more clearly in the lower-latitude provinces, with pronounced depth boundaries at around 100 m, 300 m, and 1000 m (Fig. 5). The percentage of species with distribution endpoints at these boundaries was, however, always lower than the percentage observed at the boundaries between biogeographical provinces and seldom exceeded 10% of the species present.

DISCUSSION

The boundaries between geographical provinces for both benthic taxa and pelagic taxa tended to occur in association with major oceanographic processes (e.g.

upwelling areas, river discharges, main currents, oceanographic fronts). For a large number of taxa these boundaries were characterized by pronounced changes in the oceanographic features of the waters (e.g. temperature, salinity, productivity), which generally result in different biogeographical provinces, not only in the Atlantic but also in the world's other oceans (Briggs, 1974; Margalef, 1974; Zezina, 1997; Longhurst, 1998). The boundaries in the pelagic taxa coincide with clear transitional oceanic domains, according to the biogeochemical provinces defined by Longhurst *et al.* (1995). The patterns in benthic taxa are mainly influenced by the Sahara and Benguela

Table 4. Mean range size (standard deviation, SD, in parentheses) and skewness of the distributions by biogeographical provinces and pairwise comparisons (Mann–Whitney *U*-test and Kolmogorov–Smirnov test) among provinces in benthic taxa from the eastern Atlantic. Only contiguous provinces are considered in pairwise comparisons, and provinces with less than ten species are not analysed (level of significance, $P < 0.05$). N = number of species and number of endemism (in parentheses) by province. Skewness is obtained from \log_{10} transformed measures of range size (* <0.05 , ** <0.01 , *** <0.001 , NS = non-significant). The designation of biogeographical provinces mainly follows Longhurst *et al.* (1995) and Longhurst (1998): SARC = Atlantic Subarctic, NECS = North-east Atlantic Continental Shelf, CNRY = Canary Current Coastal, GUIN = Guinea Current Coastal, BENG = Benguela Current Coastal

Group		SARC (S) 80°N–70°N	NECS (N) 70°N–50°N	CNRY (C) 50°N–20°N	GUIN (G) 20°N–15°S	BENG (B) 15°S–35°S	Mann– Whitney	Kolmogorov– Smirnov
Cephalopoda	N	2 (1)	20	18 (7)	26 (6)	12 (9)		
	Mean (SD)	35.0 (14.1)	53.6 (22.9)	46.4 (31.3)	47.2 (22.7)	42.8 (36.6)	all NS	all NS
	Skewness		–0.63 ^{NS}	0.05 ^{NS}	–2.19 ^{***}	0.07 ^{NS}		
Stomatopoda	N	–	2	16	25	1		
	Mean (SD)	–	17.5 (3.5)	34.9 (15.5)	28.8 (15.7)	13.0	all NS	all NS
	Skewness			–0.86 ^{NS}	–2.18 ^{***}			
Decapoda								
	Coastal	N	9 (1)	109 (6)	307 (88)	325 (145)	45 (21)	
		Mean (SD)	37.8 (20.0)	33.9 (17.9)	27.9 (16.8)	26.9 (16.7)	42.2 (16.0)	$N > C, G < B$
		Skewness		–0.33 ^{NS}	–0.56 ^{***}	–0.49 ^{***}	0.11 ^{NS}	N-C, G-B
	Shelf/Slope	N	20 (1)	71 (2)	150 (9)	126 (30)	62 (24)	
		Mean (SD)	36.4 (37.4)	61.6 (94.5)	53.7 (70.3)	53.7 (72.1)	56.9 (33.7)	all NS
		Skewness	1.07*	0.77**	0.19 ^{NS}	0.24 ^{NS}	–0.50 ^{NS}	all NS
Pisces								
	Coastal	N	56 (4)	180 (5)	655 (143)	557 (254)	143 (15)	
		Mean (SD)	27.6 (12.7)	36.7 (22.9)	35.3 (22.9)	31.3 (24.5)	15.6 (10.8)	$C > G, G > B$
		Skewness	–1.29 ^{***}	–1.08 ^{***}	–1.39 ^{***}	–0.95 ^{***}	–0.90 ^{***}	S-N, N-C, C-G
	Shelf/Slope	N	102 (8)	210 (9)	309 (44)	241 (50)	113 (11)	
		Mean (SD)	32.2 (21.8)	48.2 (27.7)	43.9 (26.4)	46.2 (29.4)	64.3 (29.7)	$S < N, G < B$
		Skewness	–0.74**	–1.36 ^{***}	–1.44 ^{***}	–1.25 ^{***}	–2.11 ^{***}	C-G

upwellings in the eastern Atlantic, and boundaries of Labrador and Falkland currents or Amazon river discharges in the western Atlantic. The fact that the boundaries marked the distribution ranges for a large number of species on both sides of (in the case of benthic species) and over the whole Atlantic (in the case of pelagic species) is a reflection on the general nature of the relationship between oceanographic events and biogeographical boundaries. The location, oceanographic characteristics, and changes in fauna at certain boundaries between provinces have been described by many researchers in studies both regional (Gordon & Duncan, 1985; Macpherson, 1991; Gomes, Haedrich & Villagarcia, 1995; Mahon *et al.*, 1998; Bergstad, Bjelland & Gordon, 1999; Williams, Koslow & Last, 2001; Abello, Carbonell & Torres, 2002; Gaertner, Bertrand & Souplet, 2002; Grothues *et al.*, 2002) and larger (Cartes & Sarda, 1992; Rapoport, 1994; Longhurst, 1998; Naranjo, Carballo & García-Gómez, 1998; Joyeux *et al.*, 2001) in scale. Certain boundaries, particularly those located at low and

middle latitudes, coincide with marked changes in species richness in the taxa considered (Macpherson, 2002). The location of the boundaries does not affect coastal, shelf/slope, and slope/rise species in the same way. The effect of the oceanographic events marking the biogeographical boundaries on the shelf and slope is much lower on the broad slope/rise plains, and in consequence the boundaries are poorly defined, which corroborates the low level of zonation in the slope/rise region (Haedrich, Rowe & Polloni, 1980; Gordon & Duncan, 1985; Haedrich & Merrett, 1990). However, the geographical distributions of many deep-sea species have numerous uncertainties, and any conclusion on these species is still almost speculative.

Range size generally tended to be larger for the pelagic taxa than for the benthic taxa. These differences were also discernible in the range size distribution shapes. Distributions for the pelagic species tended to be left-skewed and significantly different from lognormal on log transformation of the data. Most benthic species had relatively small range

Table 5. Mean range size (standard deviation, SD, in parentheses) and skewness of the distributions by biogeographical provinces and pairwise comparisons (Mann–Whitney *U*-test and Kolmogorov–Smirnov test) among provinces in benthic taxa from the western Atlantic. Only contiguous provinces are considered in pairwise comparisons, and provinces with less than ten species are not analysed (level of significance, $P < 0.05$). N = number of species and number of endemism (in parentheses) by province. Skewness is obtained from \log_{10} transformed measures of range size (* < 0.05 , ** < 0.01 , *** < 0.001 , NS = non-significant). The designation of biogeographical provinces mainly follows Longhurst *et al.* (1995) and Longhurst (1998): ARCT = Atlantic Arctic, NWCS = North-west Atlantic Continental Shelf, CARB = Caribbean, GUIA = Guiana Current Coastal, BRAZ = Brazil Current Coastal, ANTA = Antarctic

Group		ARCT (A) 80°N–70°N	NWCS (N) 70°N–35°N	CARB (C) 35°N–10°N	GUIA (G) 10°N–25°S	BRAZ (B) 25°S–55°S	ANTA (AN) 55°S–70°S	Mann–Whitney	Kolmogorov–Smirnov
Cephalopoda	<i>N</i>	4 (2)	21 (5)	34	30	25	6		
Mean (SD)		32.8 (15.6)	49.7 (25.8)	42.1 (24.4)	41.7 (23.6)	42.9 (26.5)	44.2 (35.6)	all NS	all NS
Skewness			-0.84 ^{NS}	-0.61 ^{NS}	-0.57 ^{NS}	0.02 ^{NS}			
Stomatopoda	<i>N</i>	-	4 (1)	66 (8)	13 (2)	3	-		
Mean (SD)		-	27.5(25.3)	23.3 (18.4)	42.1 (20.3)	15.0 (5.0)	-	all NS	all NS
Skewness			0.01 ^{NS}		-1.00 ^{NS}				
Decapoda									
Coastal	<i>N</i>	2	71 (5)	621 (302)	347 (37)	82 (8)	-		
Mean (SD)		34.3 (6.0)	38.4 (25.1)	29.7 (21.7)	43.0 (20.2)	39.5 (24.7)	-	N > C, C > G	N-C, C-G, G-B
Skewness			0.14 ^{NS}	-0.68 ^{***}	-1.75 ^{***}	0.81 ^{NS}			
Shelf/Slope	<i>N</i>	16	44 (1)	283 (107)	173 (3)	34 (2)	11 (3)		
Mean (SD)		32.9 (5.2)	37.3 (17.1)	26.6 (18.0)	33.8 (18.8)	33.0 (24.5)	20.0 (5.9)	N < C, C < G	N-C, C-G
Skewness		-0.13 ^{NS}	-0.54*	-0.54 ^{***}	-0.81 ^{***}	-0.27 ^{NS}	-0.60 ^{NS}		
Pisces									
Coastal	<i>N</i>	12	225 (34)	875 (537)	461 (108)	131 (24)	3 (2)		
Mean (SD)		33.3 (6.5)	27.9 (8.4)	34.8 (22.8)	53.0 (16.2)	46.7 (25.6)	21.7 (11.6)	C < G, G > B	N-C, C-G, G-B
Skewness		-1.81*	-0.32 ^{NS}	-0.29 ^{***}	-1.23 ^{***}	-0.71 ^{***}			
Shelf/Slope	<i>N</i>	13 (1)	173 (38)	379 (137)	208 (35)	213 (85)	57 (50)		
Mean (SD)		30.2 (8.3)	43.9 (26.4)	36.3 (24.9)	50.1 (25.6)	41.1 (25.2)	38.9 (13.2)	N > C, C < G, G > B, B > AN	N-C, C-G, G-B, B-AN
Skewness		-0.92 ^{NS}	0.06 ^{NS}	-0.99 ^{***}	-0.94 ^{***}	-0.02 ^{NS}	4.00 ^{***}		

Table 6. Correlation between the latitude furthest from the equator (north or south) in each species' latitudinal distribution and latitude range. (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS = non-significant)

	<i>N</i>	<i>R</i>
PELAGIC GROUP		
Hydromedusae		
Holoplanktonic	64	0.24*
Meroplanktonic	230	0.17*
Siphonophorae	107	0.45***
Chaetognatha	41	0.66***
Appendicularia	60	0.30*
Salpida	31	0.46**
Cephalopoda	132	0.10 ^{NS}
Euphausiacea	41	0.05 ^{NS}
Decapoda	105	0.50***
Pisces	451	0.69***
BENTHIC GROUP		
Cephalopoda		
Eastern	56	0.22 ^{NS}
Western	55	0.05 ^{NS}
Stomatopoda		
Eastern	29	0.54*
Western	69	0.10 ^{NS}
Decapoda		
Coastal (E)	489	0.47***
Shelf/Slope (E)	116	0.22*
Slope/Rise (E)	77	0.14 ^{NS}
Coastal (W)	713	0.46***
Shelf/Slope (W)	317	0.22***
Slope/Rise (W)	38	0.05 ^{NS}
Pisces		
Coastal (E)	827	0.39***
Shelf/Slope (E)	439	0.20***
Slope/Rise (E)	43	0.48***
Coastal (W)	1220	0.32***
Shelf/Slope (W)	586	0.20***
Slope/Rise (W)	126	0.26***

sizes, while a few had relatively large ones. These ranges were not different from lognormal, and only Pisces had a significantly left-skewed distribution on being log transformed. These same patterns were likewise observed on analysing each taxon separately by biogeographical province. Nevertheless, interesting exceptions were found, such as that for Antarctic Pisces, being distinctly right-skewed due to the high endemism rate (Gon & Heemstra, 1990) and hence not observed for any other taxon or province. These results corroborate the special characteristics and relative isolation of Antarctic benthic ecosystems that have been reported by a number of workers (Arntz & Gili, 2001; Gray, 2001; and references cited therein).

Table 7. Benthic taxa. Relationship (Spearman's regression coefficient) between depth range size and maximum depth of occurrence (N = number of species)

	<i>N</i>	R^2	<i>P</i>
Cephalopoda			
Eastern	56	0.92	<0.0001
Western	57	0.91	<0.0001
Stomatopoda			
Eastern	29	0.95	<0.0001
Western	69	0.93	<0.0001
Decapoda			
Eastern	678	0.89	<0.0001
Western	1067	0.82	<0.0001
Pisces			
Eastern	1319	0.96	<0.0001
Western	1965	0.96	<0.0001

Table 8. Skewness (data \log_{10} transformed) of the depth range size distributions of benthic taxa (Crustacea Decapoda and Pisces), by biogeographic provinces in both sides of the Atlantic Ocean. (Skew different from log normal distribution: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS = non-significant)

Province	Decapoda	Pisces
EASTERN ATLANTIC		
Atlantic Subarctic	-0.26 ^{NS}	-0.91***
North-east Continental Shelf	-0.13 ^{NS}	-0.35**
Canary Current Coastal	0.06 ^{NS}	-0.09 ^{NS}
Guinea Current Coastal	0.38**	0.16 ^{NS}
Benguela Current Coastal	-0.51 ^{NS}	-0.11 ^{NS}
WESTERN ATLANTIC		
Atlantic Arctic	-0.53*	0.16 ^{NS}
North-west Continental Shelf	0.34**	0.44***
Caribbean	0.66***	0.72***
Guiana Current Coastal	0.69***	0.90***
Brazil Current Coastal	-0.19 ^{NS}	0.07 ^{NS}
Antarctic	-0.70*	-0.69*

There have been numerous examples of the lognormal distributions of geographical range sizes, primarily for terrestrial groups (e.g. Pagel *et al.*, 1991; Ruggiero, 1994; Brown *et al.*, 1996; Gaston & Blackburn, 1996, 2000; Gaston, 1998; Hecnar, 1999) but also for marine groups (e.g. Hansen, 1980; Jablonski, 1987; Roy *et al.*, 1994), although these have not been so numerous. Nevertheless, in various cases the distributions have been clearly left-skewed. The findings reported by these other researchers, together with the findings of the study reported here, bear out the conclusions of Brown *et al.* (1996) and Gaston (1998), who have claimed that these two types of distribution are

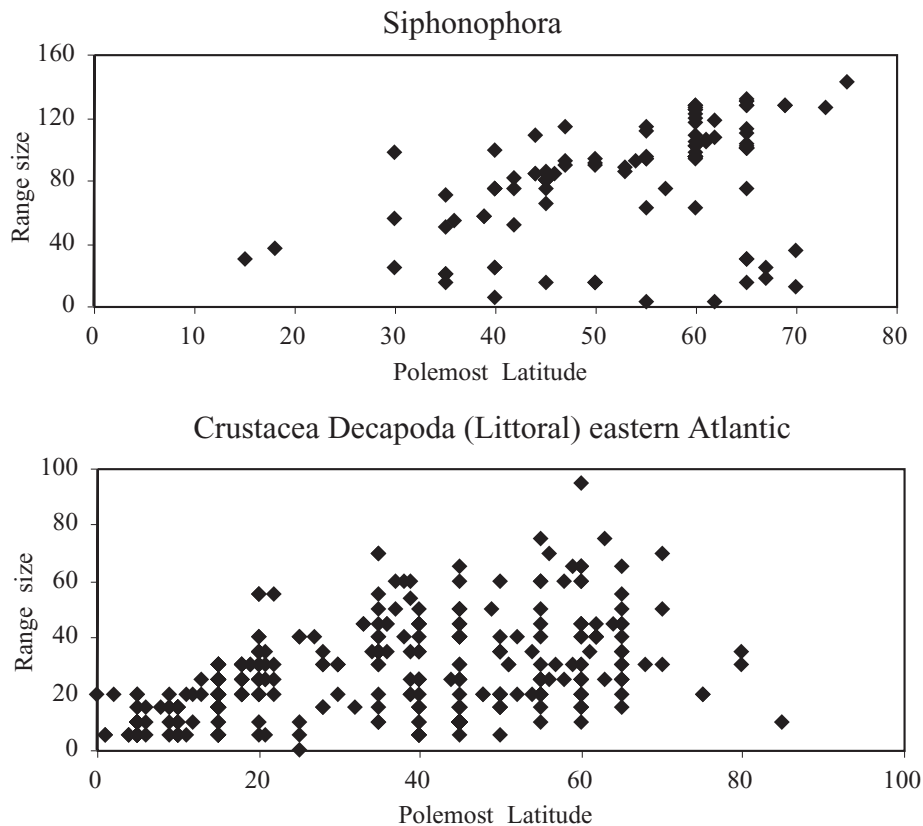


Figure 4. Relationship between the latitude furthest from the Equator (north or south) in each species' latitudinal distribution and its latitudinal range size in Siphonophora (along the Atlantic Ocean) and benthic coastal Decapoda (along the eastern Atlantic). Range in degrees of latitude.

the most prevalent in nature. The higher frequency of left-skewed distributions in the pelagic taxa suggests that this type of distribution is better suited to taxa with higher dispersal capabilities as larvae or adults which occupy large biogeographical provinces, while lognormal distributions are predominant for taxa composed of species which are less capable of dispersal and occupy smaller provinces (e.g. some benthic groups).

The results set out in this study are indicative of a certain tendency on the part of those species in each taxon with distributions that reach latitudes closest to the poles to have the broadest ranges. Although the explained variance in these relationships between range and the endpoint closest to a pole was low, this tendency was observed in most of the groups considered, suggesting that Rapoport's rule does hold but that this rule is not the sole effect responsible for latitudinal patterns in range sizes. By the same token, the tendencies resulting from the pairwise comparisons between provinces did not support the existence of a generalized Rapoport's rule for all taxa.

The ranges for benthic species inhabiting the tropical provinces in the eastern Atlantic were smaller than

those for species dwelling at higher latitudes. On the other hand, the trend in the western Atlantic was the converse. Similarly, benthic species inhabiting the Arctic and Antarctic provinces tended to have smaller ranges than species dwelling at latitudes further from the poles, because of the high endemism rate in these provinces. The pattern observed for most of the pelagic taxa was for the species inhabiting the central Atlantic province to tend to have smaller ranges than species dwelling closer to the poles and for the endemism rate to decrease from low latitudes to high. The importance of endemism in studies on Rapoport's rule was made apparent by Roy *et al.* (1994), who showed that broad provinces tended to have more endemic species with small ranges than narrow provinces, giving rise to an inverse relationship between province size and mean species range. This was not clearly observable for the taxa considered in this study. But nevertheless latitudinal trends in the endemism rate in each province may help explain some of the patterns emerging. Where the rate decreased from the Equator to the poles, significant differences between the provinces tended to follow Rapoport's rule (pelagic taxa), whereas where the level

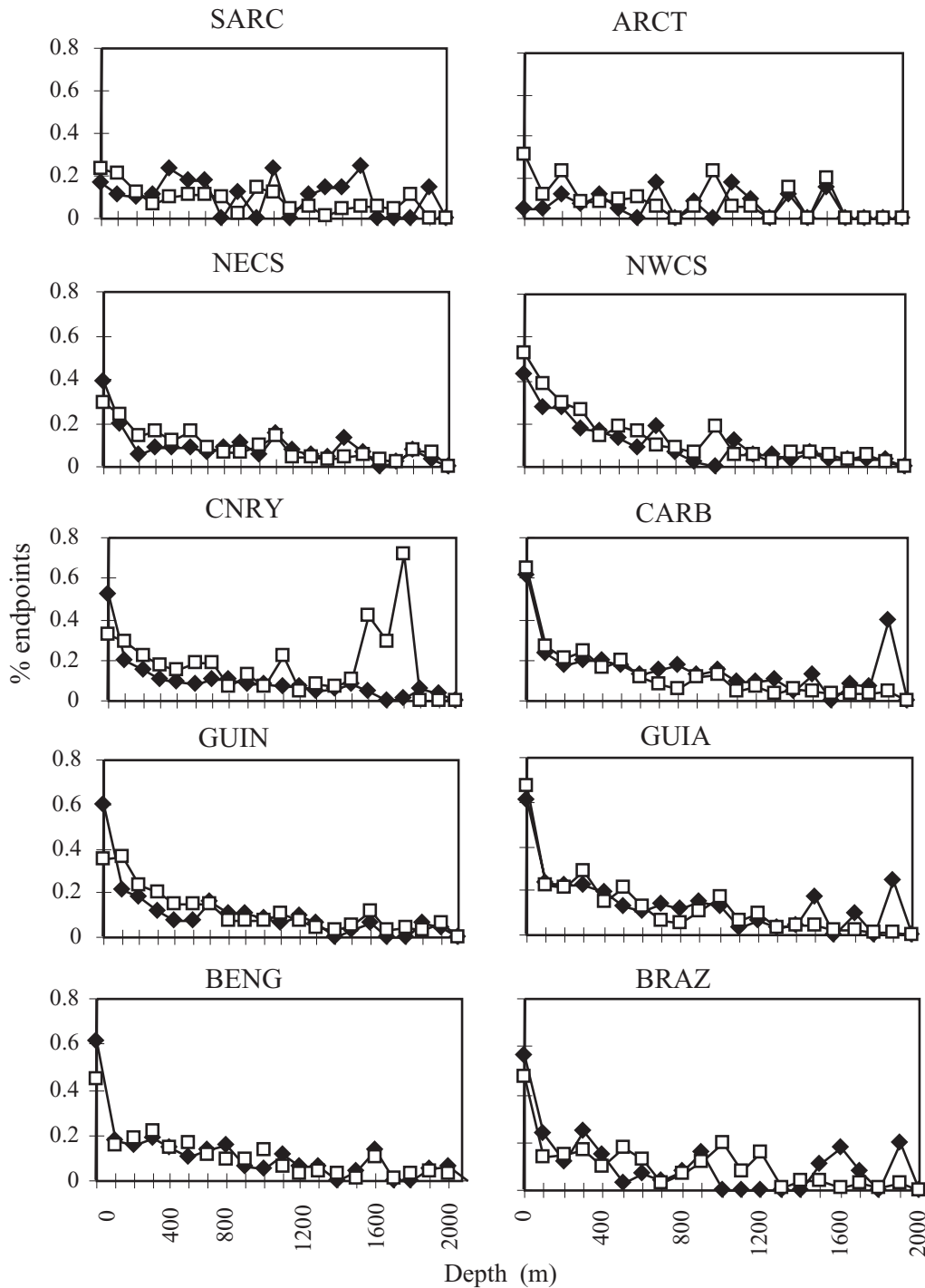


Figure 5. Distribution of the depth endpoints of benthic taxa (Crustacea Decapoda, squares; Pisces, diamonds) by biogeographical provinces on the eastern and western Atlantic Ocean, binned by 100 m of depth. Each point represents the ratio, as a percentage, of species whose depth distribution endpoints fell within any given 100 m bin to the total number of species present at that bin. Occurrences deeper than 2000 m are not considered. The designation of biogeographical provinces mainly follows Longhurst *et al.* (1995) and Longhurst (1998) (see text). Eastern Atlantic: SARC = Atlantic Subarctic, NECS = north-east Atlantic Continental Shelf, CNRY = Canary Current Coastal, GUIN = Guinea Current Coastal, BENG = Benguela Current Coastal. Western Atlantic: ARCT = Atlantic Arctic, NWCS = north-west Atlantic Continental Shelf, CARB = Caribbean, GUIA = Guiana Current Coastal, BRAZ = Brazil Current Coastal.

did not decrease the significant differences did not always follow that rule (benthic taxa). These results emphasize the important role played by the endemism rate in determining whether or not Rapoport's rule will hold (see also Roy *et al.*, 1994).

Gaston & Blackburn (2000) considered various mechanisms that might explain latitudinal gradients in range size (climatic variability, area size, extinction rate, competition, and biogeographical boundaries) and showed that the climatic variability hypothesis was the one that best accounted for whether or not Rapoport's rule applied. Other authors (e.g. Rohde, 1996) suggest that the existence of the rule may be the result of selection for tolerance to greater temperature fluctuations. As originally proposed by Stevens (1989), it was postulated that the greater seasonal environmental variation at higher latitudes requires the species living there to have broader tolerances, thereby enabling those species to adapt to a wider range of climates than species dwelling closer to the Equator. Different investigators (e.g. Rohde *et al.*, 1993; Roy *et al.*, 1994; Gaston & Blackburn, 2000) have pointed out that this hypothesis could explain the broad ranges of cold-water species but not the broad ranges of many tropical species. Similarly, it fails to account for the high endemism rate, with species with small range sizes, in waters near the poles. As Gaston & Blackburn (2000) have suggested, latitudinal patterns in range size may be better explained by the reasonably constant environmental conditions within a given province and the distinct environmental differences that separate two adjacent provinces, e.g. temperature, salinity, and productivity (Rutherford *et al.*, 1999; see also Roy *et al.*, 1994 and Rohde, 1996) rather than by variations in climatic conditions. The factors that best account for latitudinal gradients in range size are boundary location, environmental conditions at the boundaries, and the ability of species to cross the boundaries.

The mechanisms which allow a species to cross these boundaries or which prevent them from doing so, thereby determining its range size, have not been adequately studied. Some studies that have tried to relate larval dispersal capacity and range size or dispersal capacity and gene flow have yielded inconclusive results (Doherty, Planes & Mather, 1995; Victor & Wellington, 2000; Raventos & Macpherson, 2001). This all suggests that latitudinal patterns in range size are caused by complex mechanisms which have not been examined in any great detail at large scales and which are therefore in need of future research (see also Gaston *et al.*, 1998).

Patterns in the depth distributions of marine species have been studied for decades now (e.g. Vinogradova, 1959, 1997), and there is a large body of work relating vertical range, depth of occurrence, and vertical environmental gradients (e.g. Ekman, 1953;

Knudsen, 1970; Hansen, 1975; Sanders, 1979; Rex, 1981; Etter & Rex, 1990; Gage & Tyler, 1991; Pineda, 1993; Macpherson & Duarte, 1994; Stevens, 1996; Merret & Haedrich, 1997; Smith & Brown, 2002). Boundaries between depth provinces are usually related to environmental variations associated not just with temperature but also with productivity, hydrodynamics, and other oceanographic parameters (Haedrich & Merrett, 1990; Macpherson, 1991; Abello *et al.*, 2002). These depth boundaries define a coastal domain (c. <100 m), a continental shelf and slope domain (c. 100–1000 m), ordinarily with a boundary in the vicinity of the shelf break (c. 300 m) and a slope/rise domain (>1000 m). The extent of these domains changes with latitude, because environmental conditions tend to be more uniform over depth towards the poles (Zezina, 1997; Longhurst, 1998). The differences in the size of the different depth provinces regulate the depth range of most species, with a clear relationship among depth of occurrence, depth range, and latitude (see also Stevens, 1996).

The negative relationship between depth of occurrence and depth range has been pointed out by numerous authors working on marine biogeography (e.g. Ekman, 1953; Vinogradova, 1959; Knudsen, 1970; Hansen, 1975). This clear relationship shows that species subject to greater environmental fluctuation (i.e. coastal species) have smaller depth ranges, while species dwelling in less variable environments (i.e. slope/rise species) have larger ranges (Pineda, 1993; Smith & Brown, 2002). These findings stand in contrast to the hypothesis originally postulated by Stevens (1989), but they underscore the importance of province size and the existence of clear boundaries to range size distributions. Latitudinal changes in the skewness of depth range size distributions (left-skewed at high latitudes and right-skewed at low latitudes) can be related to latitudinal changes in depth zonation and lend support to the climatic variability hypothesis as modified by Roy *et al.* (1994) and Gaston & Blackburn (2000) to explain variations in species' distribution ranges. Separations between depth provinces are not as pronounced as separations between latitudinal provinces, as evidenced by the low proportion of species with distribution endpoints at a depth boundary as compared to the higher proportion of species with distribution endpoints at a latitudinal boundary. This suggests that the environmental or biological mechanisms regulating the latitudinal distribution of species have a greater global effect than the mechanisms regulating depth distribution.

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