

# Deep-sea coral distribution on seamounts, oceanic islands, and continental slopes in the Northeast Atlantic

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## Abstract

A database of deep-water (> 200 m) antipatharians, scleractinians, and gorgonians has been assembled for the NE Atlantic to determine what their distribution and diversity was before coral habitats became heavily impacted by bottom fishing gear. Benthic sampling expeditions from 1868–1985 have provided 2547 records showing the deep-water distribution of 22 species of antipatharians, 68 species of scleractinians, and 83 species of gorgonians with the majority of records found from seamounts, oceanic islands, and the continental slope of the warm temperate region. Too little is known about the coral biota of boreal and tropical seamounts to assess their levels of endemism, but on seamounts in the warm temperate region of the NE Atlantic the level of endemism in antipatharian, scleractinian and gorgonian corals is low (< 3%). Many of the species found on seamounts are characteristic of oceanic islands in this region and the oceanic islands have a significantly different coral fauna to that recorded at the same depths on the continental slope. Given the key role that corals can play in structuring deep-sea habitats it is hoped that our database will help inform the development of a network of marine protected areas to provide long-term protection for the differing communities found on continental slopes and isolated offshore habitats.

A surge of international research into seamount ecology (Malakoff, 2003; Pitcher et al., 2007) was recently boosted by work on South Pacific seamounts reporting that > 30% of the species found were new to science and potentially endemic to seamounts (Parin et al., 1997; Richer de Forges et al., 2000). Surveys to date show that deep-water coral communities often characterize seamount habitats and that these communities have been heavily impacted by trawling (Koslow et al., 2001; Rogers et al., 2007). The North Atlantic has the longest and most intensive history of biogeographic research, yet even there most seamounts remain unsampled (Stocks et al., 2004) and coral reefs several km in extent have only recently been discovered (Fosså et al., 2005). At the same time as these amazing discoveries are being made, benthic surveys are revealing the increasing extent to which bottom-trawling is altering the habitats of deep-sea corals worldwide (Hall-Spencer et al., 2002; Clark and O'Driscoll, 2003). This is of particular concern considering that deep-water corals are amongst the longest lived and slowest growing organisms on Earth (Roark et al., 2006). In most parts of the world offshore expansion of the bottom-trawling industry began before any habitat assessment had taken place (Gordon, 2003). Fortunately, there is a wealth of historical deep-water coral data for the NE Atlantic providing detailed records dating back to the expeditions of the vessels LIGHTENING, PORCUPINE, and JOSEPHINE (1868–1869). Regular sampling expedi-

tions such as those funded by Prince Albert I of Monaco from 1886–1915 provide a rich source of information on the coral fauna (e.g., Studer, 1901; Thomson, 1927).

Deep-water bottom-trawling was pioneered in the North Atlantic by the Russians in the 1970s targeting *Coryphaenoides rupestris* Gunnerus, 1765 (roundnose grenadier) south of Iceland and on the Reykjanes Ridge, but it was not until the late 1980s that deep-water bottom-trawling began to increase rapidly along the European continental slope with the development of new markets for *Molva dypterygia* (Pennant, 1784) (blue ling), *Aphanopus carbo* Lowe, 1839 (black scabbardfish), and *Hoplostethus atlanticus* Collett, 1889 (orange roughy) (Gordon, 2001, 2003). Deep-water trawling is now common, with trawl tracks clearly visible on acoustic images and seabed photographs of the European continental slope (Hall-Spencer et al., 2002). Damage continues partly because coral-rich areas are poorly mapped, so trawlers do not know the key sites to avoid, and partly because only very small areas are closed to bottom-trawling (Butler, 2005; Wheeler et al., 2005).

We aim to build on the approach adopted by Cairns and Chapman (2001) and Watling and Auster (2005), drawing attention to valuable baseline information on the diversity and distribution of deep-water scleractinian, gorgonian and antipatharian corals before bottom-trawling became widespread. We have collated a “pre-1985” database of deep-water corals of the NE Atlantic and use it to compare coral faunas on seamounts, continental slopes, and oceanic islands of the warm temperate region.

## Methods

We restricted our analyses to scleractinian, antipatharian, and gorgonian corals because these are the most commonly recorded coral groups in the NE Atlantic, providing the richest source of biogeographic data for our comparisons of seamount, continental slope, and oceanic island habitats. The following publications were used as sources of historical data on the distributions of NE Atlantic scleractinian, antipatharian, and gorgonian corals: Grasshoff (1972, 1973, 1977, 1981a,b,c, 1985a,b, 1986, 1989), Arnaud and Zibrowius (1973), Zibrowius (1973, 1980, 1985), Grasshoff and Zibrowius (1983), Keller (1985), Pasternak (1985), Tendal (1992), Tyler and Zibrowius (1992), Rogers (1999), and Molodtsova (2006), in addition to the original cruise reports of the Prince of Monaco expeditions 1886–1915 held at the United Kingdom’s National Marine Biological Library in Plymouth. We updated historical synonyms following the high-level taxonomic nomenclature used for octocorals by Williams and Cairns (<http://www.calacademy.org/research/izg/OCTOCLASS.htm>, accessed September 2006) and the species-level nomenclature given by the UNESCO-IOC register of marine organisms (<http://annual.sp2000.org/2006/search.php>, accessed September 2006) together with Molodtsova (2006) for the most recently described antipatharians. Our database has been made available through Seamounts Online (<http://seamounts.sdsc.edu>), an open-access portal for deep-sea data.

Coral data (taxon, position, depth, date collected, cruise details, and other notes) were entered into a Microsoft Access database—some scleractinians were recorded as dead at the time of collection and these were excluded from further analyses because they could have been fossil occurrences of species no longer living at the sites in question. Those records from > 200 m depth which provided a latitude and longitude position were plotted using ArcView GIS to show the distribution of historical scleractinian, antipatharian, and gorgonian records on a General Bathymetric Chart of the Oceans (GEBCO) showing known seamounts, continental slope areas, and oceanic islands in an area from 12°N–62.5°N and 10°E–40°W. We classified seamounts as topographic rises with limited extent across the summit which are > 1000 m elevation (derived from the December 2005 GEBCO seamount list: [http://www.ngdc.noaa.gov/mgg/gebco/gazet\\_dec2005.xls](http://www.ngdc.noaa.gov/mgg/gebco/gazet_dec2005.xls) for the area north of 35.9568°N and OASIS (2003) for seamounts south of 35.9568°N). Coral records from 200–2000 m depth around islands which rise from abyssal depths (the Azores, Ma-

deira, and the Cape Verde Islands) were classified as oceanic island data whereas records from 200–2000 m depth on the shelf and along the edge of the European continent (e.g., the Canaries and Rockall) were classified as continental slope data. Some records could not be included in the GIS database because they did not provide latitude and longitude, but we were able to use these data in analyses of the faunas of seamounts, continental slopes, and oceanic islands when they provided enough information to be able to attribute those records to a particular province (e.g., “240 m depth between Pico and Sao Jorge in the Azores” was attributed to the Azores).

The statistical package PRIMER-E (Clarke and Warwick, 2001a) was used to analyse differences in coral communities among seamounts, continental slope, and oceanic islands in the warm temperate NE Atlantic north of Mauritania and south of Cape Finisterre, as this region proved to be the most data-rich for deep-water corals. A distance matrix was produced of between-site similarities based on presence/absence data for all species at all sites, employing the Bray-Curtis similarity coefficient and a dendrogram of site similarities was produced using group-averaged clustering in PRIMER-E. The distance matrix was used to produce an ordination plot of between-site similarities using non-metric multidimensional scaling (n-MDS). Reliability of the n-MDS plot was assessed by calculating Kruskal’s stress value (Kruskal, 1964), a measure of goodness-of-fit of the plotted sample distances in the n-MDS and the calculated distances in the parent matrix. Stress values  $\leq 0.05$  give an excellent representation of the actual distances between points with no prospect of misinterpretation (Clarke and Warwick, 2001a). To further define the biodiversity at the different sites we calculated values of average taxonomic distinctness,  $\Delta^+$  (“taxonomic breadth” sensu Clarke and Warwick, 2001a) and variation in taxonomic distinctness  $\Lambda^+$  (Clarke and Warwick, 2001b) for the coral assemblages at each site.  $\Delta^+$  and  $\Lambda^+$  are calculated using the overall species list for all sites analyzed (see Clarke and Warwick, 2001a).  $\Delta^+$  of a species list is a measure of the average taxonomic distance apart of all its pairs of species, whereas  $\Lambda^+$  is a measure of variance of the taxonomic distances between pairs of species at a site around the site  $\Delta^+$  value. We then tested whether these values deviated from the expected values for a coral assemblage of known species richness drawn from the same regional fauna, using the TAXDTEST routine in PRIMER-E.

## Results

A database of 2547 pre-1985 records of deep-water corals ( $> 200$  m) was assembled for the NE Atlantic area shown in Figure 1, which included 22 species of antipatharians, 83 species of gorgonians, and 68 species of scleractinians. Most records of corals collected prior to 1985 came from the campaigns of a few research vessels such as the R/Vs METEOR, JEAN CHARCOT, and THALASSA (Table 1). Latitude and longitude data were available for 1808 of the deep-water coral records and are shown on the bathymetric map of the area in Figure 1. This map shows that most of historical coral records are clustered along the continental slope and around the oceanic islands of the Azores, Madeira, and the Cape Verde Islands. Well-sampled seamount chains to the south of the Azores and to the northeast of Madeira were also hotspots of historical coral records.

Because of a lack of sampling, very little is known about the pre-trawling coral fauna of seamounts in the cold temperate or tropical regions of the NE Atlantic. However, the warm temperate region north of Mauritania and south of Cape Finisterre has been intensively sampled and by combining data from 1869–1985 we were able to examine the overall biogeography and potential degree of endemism on seamounts in this region. Ordination showed that the composition of historical records of seamount corals was very different from records at the same depths (200–2000 m) around the islands of the Azores and Madeira and the continental slope (Fig. 2). Some of this dissimilarity is a result of apparent endemism; in our dataset of 18 species of antipatharians, 58 species of gorgonians, and 60 species of scleractinians for the warm temperate region of the

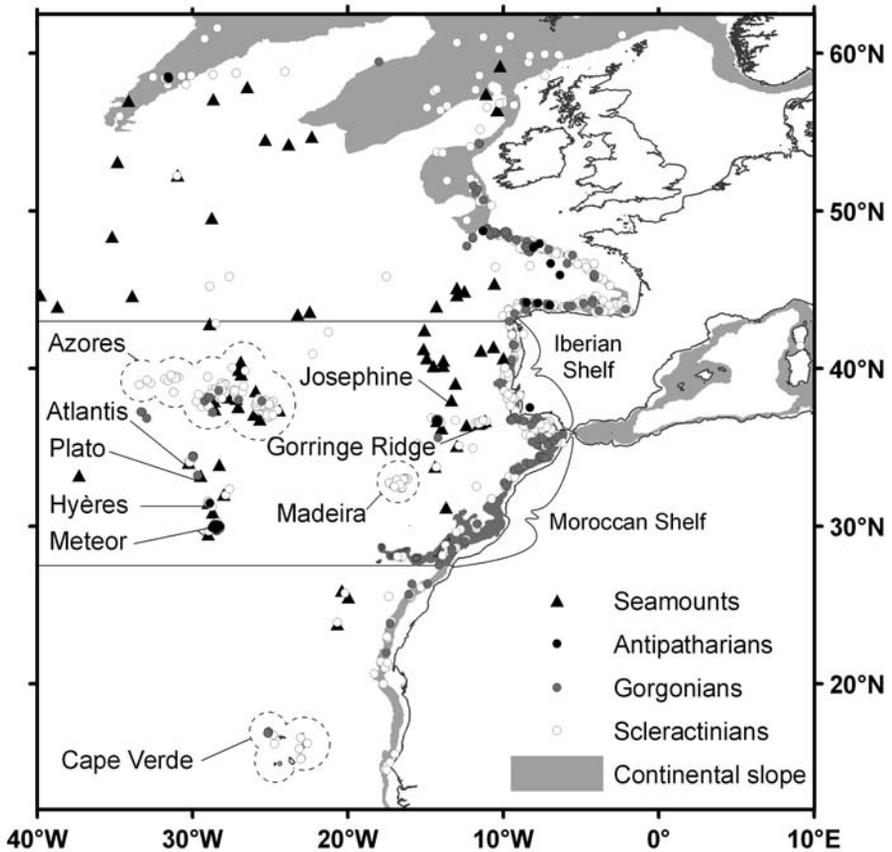


Figure 1. Georeferenced records of deep-water (> 200 m) antipatharian ( $n = 65$ ), scleractinian ( $n = 505$ ), and gorgonian ( $n = 1264$ ) corals for the NE Atlantic compiled from pre-1985 reports. Seamounts > 1000 m in height, oceanic islands, Iberian, and Moroccan continental slopes (200–2000 m) are shown. Horizontal lines delimit a data-rich area north from Mauritania to Cape Finisterre used for comparison of seamount/oceanic island/continental shelf faunas. Named seamounts had sufficient pre-1985 coral data for inclusion in our analyses.

NE Atlantic, the scleractinian *Paracyathus arcuatus* Lindström, 1877 has only been recorded on seamounts and the gorgonians *Dentomuricea meteor* Grasshoff, 1977 and *Tabigorgia cylindrica* Pasternak, 1985 to date, have only been recorded on Great Meteor seamount (Grasshoff, 1985a; Pasternak, 1985). Thus, < 3% of the antipatharian, scleractinian, and gorgonian corals recorded in the warm temperate NE Atlantic are potentially endemic to seamounts.

Cluster analysis indicated that the deep coral faunas recorded around the Azores and Madeira were 61.4% similar in composition and had strong affinities with those recorded from the warm temperate continental slope (Fig. 3). Seamounts were on average only 29% similar to the neighboring continental slope. This partly reflects the reduced sampling of seamounts but there is a suite of scleractinian species (e.g., *Caryophyllia alberti* Zibrowius, 1980, *Caryophyllia foresti* Zibrowius, 1980, *Leptopsammia formosa* Gravier, 1915, *P. arcuatus*) that have not been recorded along the continental slope but have been recorded frequently in open oceanic conditions. Conversely, species such as *Caryophyllia seguenzae* Duncan, 1873 have been found all along the continental slope

Table 1. Expeditions used as major sources of deep-water (> 200 m) data on corals for mapping NE Atlantic coral distribution in the area 12°N–62.5°N and 10°E–40°W. Total numbers of records are shown with georeferenced records in parentheses. “Other” were obtained from expeditions with < 20 coral records and from literature cited in the methods section.

Expeditions	Date	Antipatharians	Gorgonians	Scleractinians
RV JOSEPHINE	1869	0	2 (1)	19 (8)
RV PORCUPINE	1869–1870	0	0	32 (30)
PRINCE OF MONACO	1886–1915	40 (40)	169 (126)	142 (94)
RV CHALLENGER	1873	0	1 (1)	30 (21)
RV TRAVAILLEUR	1881–1883	0	20 (17)	18 (16)
RV TALISMAN	1883	0	50 (45)	51 (44)
RV CALYPSO	1958–1959	0	0	36 (18)
RV SARSIA	1958–1974	0	1 (1)	53 (41)
RV JEAN CHARCOT	1966–1976	5 (1)	66 (20)	300 (174)
RV METEOR	1967–1970	9 (4)	118 (81)	98 (90)
RV THALASSA	1967–1973	2 (2)	39 (36)	139 (123)
RV BARTLETT	1975	0	19 (15)	17 (14)
RV CRYOS	1984	0	36 (36)	0
Other	1868–1985	78 (18)	250 (126)	707 (591)
Totals		134 (65)	771 (505)	1,642 (1,264)

from Senegal to Scotland but appear not to have colonized oceanic islands or open oceanic seamounts north of Cape Verde (Fig. 4).

Our analysis of taxonomic patterns indicated that Madeira had greater variation in taxonomic distinctness ( $\Lambda^+$ ) than expected for the size of its species list ( $P = 0.012$ ); all other sites fell within the expected bounds for this measure. Greater deviations from expectation were clear for taxonomic breadth (Fig. 5): the oceanic islands had less taxonomic breadth than expected for their species list sizes (Madeira  $P = 0.004$ ; Azores  $P = 0.044$ ) as did two of the seamounts, Gorringer Ridge ( $P = 0.002$ ) and Hyères ( $P = 0.016$ ). Thus, these sites either had lower high-level (e.g., families, orders) taxonomic variation, or more low-level (species) taxonomic variation than expected given the composition of the database and their relative species richnesses. This low taxonomic breadth suggests proliferation of taxa in a few genera, whereas other genera from different higher families or orders remain relatively species poor. Seamounts emerge as impoverished vs the island sites in terms of species richness, but only Hyères and Gorringer Ridge had a coral fauna that fell outside limits of taxonomic breadth predicted from the taxonomic composition of the regional fauna.

## Discussion

The NE Atlantic has the best available historical data on deep-water corals, dating back to the first descriptions of life in the deep-sea (Duncan, 1873), but the records are dispersed in specialist publications, written in a variety of languages, and differ in their use of taxonomic nomenclature. The UNESCO-IOC register of marine organisms (<http://annual.sp2000.org/2006/search.php>) allowed us to use historical reports to construct a database of > 2500 pre-1985 records of antipatharians, gorgonians, and scleractinians recorded in the NE Atlantic. This database provides valuable insights into the biogeography of these corals before the impacts of deep-water trawling became widespread. Although the geographic precision of the records vary, from detailed latitude/longitude

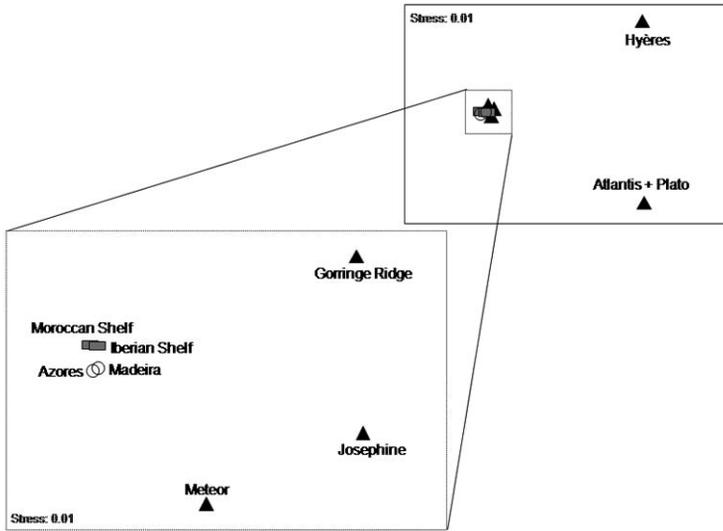


Figure 2. n-MDS ordination of coral assemblages in the warm temperate NE Atlantic north of Mauritania and south of Cape Finisterre. Ordination based upon Bray-Curtis similarity values calculated using species presence/absence. ▲ = seamounts, ■ = continental shelf slope, ○ = oceanic islands. An expanded view of the relationships amongst sites contained within the inset box is provided to facilitate interpretation.

positions to more vague information in the oldest cruise reports such as “Bay of Biscay” or “NW Flores, Azores”, the data nevertheless allow comparisons of the distribution of the species present.

Our GIS map of georeferenced data indicates that the vast majority of deep-sea coral records come from steeply-sloping seabed types around seamounts and oceanic islands and along the continental slope. This is to be expected since high relief topography provides the hard substrata that antipatharian, scleractinian, and gorgonian corals require for attachment. Habitats with abrupt changes in topography also accelerate the flow of oceanic water masses, increasing food supply to filter-feeding communities and preventing their burial in silt (Rogers, 1994, 1999; Rogers et al., in press). The Mid-Atlantic Ridge appears to be a strong biogeographic boundary between corals that characterize the American boreal continental slope and those that live in the north-flowing warmer waters on the European continental slope. Cairns and Chapman (2001) and Watling and Auster (2005) point out striking dissimilarities between the deep-water coral faunas of the eastern and western Atlantic and work by Schröder-Ritzrau et al. (2005) indicates that the palaeoceanographic history of the North Atlantic may be key to the high levels of coral biodiversity recorded in deep-water in the warm temperate NE Atlantic. They found that seamounts off NW Africa, the low-latitude Mid-Atlantic Ridge and the Azores have supported coral growth for the past 50,000 yrs whereas the last glacial maximum was associated with conditions that were unsuitable for coral growth in more northern parts of the Atlantic.

It is useful to assess the degree of endemism on seamounts in this region, given that recent data on South Pacific seamounts indicates that > 30% of the species found are potentially endemic to seamounts (Parin et al., 1997; Richer de Forges et al., 2000). As with the majority of seamounts world-wide (Stocks et al., 2004), those in the cold tem-

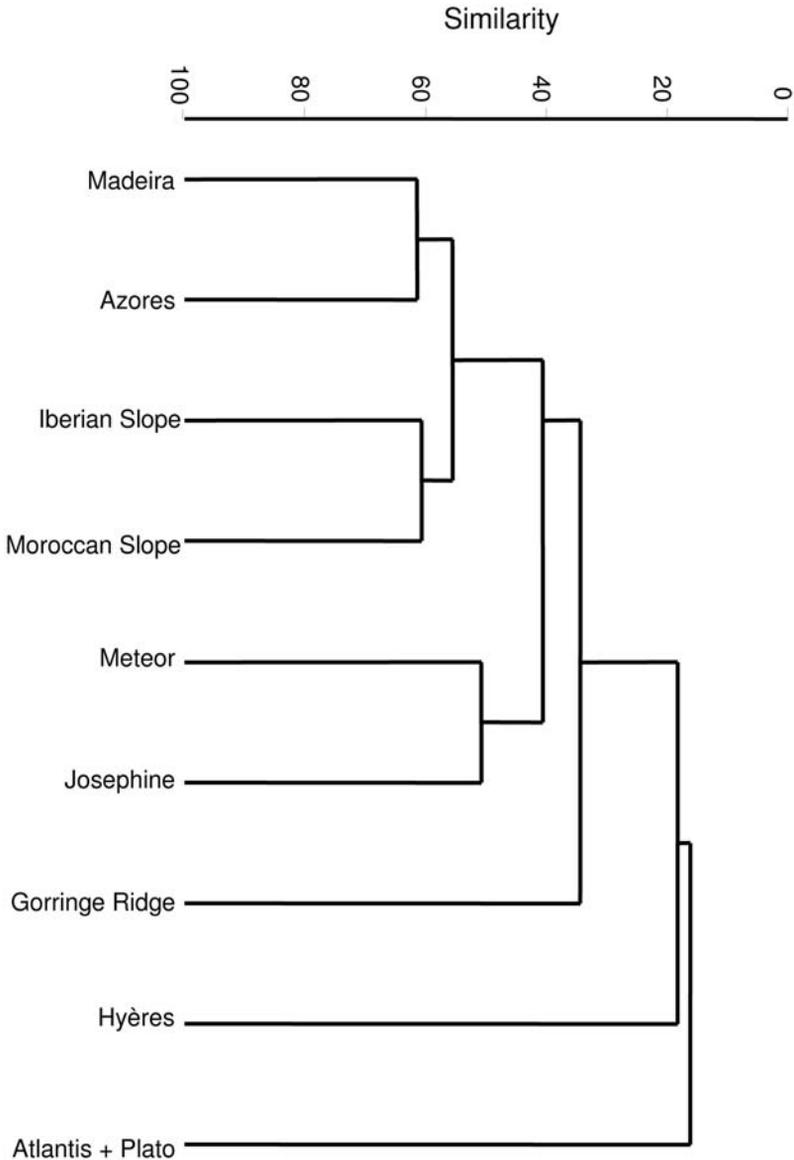


Figure 3. Group-averaged cluster plot of coral assemblages from 200–2000 m depth in the warm temperate NE Atlantic, based upon Bray-Curtis similarity values calculated from species presence/absence data.

perate and tropical regions of the NE Atlantic have been poorly studied and have few historical coral records. However, GIS mapping revealed that seamount chains south of the Azores and NE of Madeira have detailed baseline information on coral distributions allowing a comparison with the faunas found elsewhere in the warm temperate region of the NE Atlantic. We found that < 3% of the 136 species of antipatharians, gorgonians, and scleractinians known to occur in the NE Atlantic region appear to be endemic to seamounts. It is possible, in fact, that there may be no endemism on NE Atlantic seamounts; *D. meteor* and *T. cylindrica* have only been recorded on Great Meteor seamount (Grasshoff, 1985a; Pasternack, 1985) but they could occur elsewhere given that Great

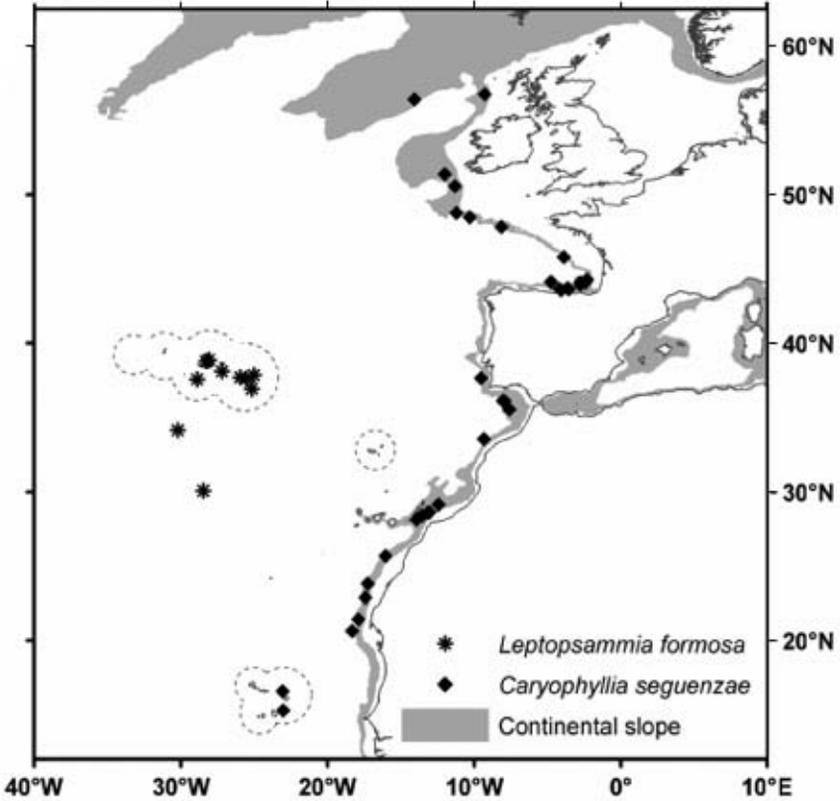


Figure 4. Pre-1985 NE Atlantic records showing the shelf-slope vs open ocean affinities of *Caryophyllia seguenzae* vs *Leptopsammia formosa*.

Meteor is part of a seamount chain that would be expected to facilitate the dispersal of corals. In the light of these results it is possible that the degree of endemism on South Pacific seamounts may be far lower than the 30% estimate of Parin et al. (1997) and Richer de Forges et al. (2000) and that these estimates reflect a lack of sampling in the deep-sea of the South Pacific region.

Despite the low levels of endemism recorded on NE Atlantic seamounts, our analyses reveal that the coral communities present are significantly different from those recorded on the continental slope. For example, the offshore islands and seamounts have a suite of species that do not occur along the continental slope. The coral fauna of seamounts in the region appears to be depauperate compared with those found on oceanic islands and the continental slope which both present larger “targets” for colonization by the planktonic phases in the coral life history. Most of the scleractinian corals of the warm temperate region are widespread (Cairns and Chapman, 2001) and are found on oceanic islands, seamounts, and shelf slope sites, although there are exceptions such as *L. formosa* which appears to be restricted to open ocean areas, away from the continental slope. Molodtsova (2006) notes that several NE Atlantic antipatharians appear to be restricted to open ocean areas, with *Antipathes erinaceus* (Roule, 1905), *Distichopathes* sp., *Phanopathes* sp., and *Stauropathes punctata* (Roule, 1905) only recorded on Josephine seamount, the Azores and Cape Verde Islands.

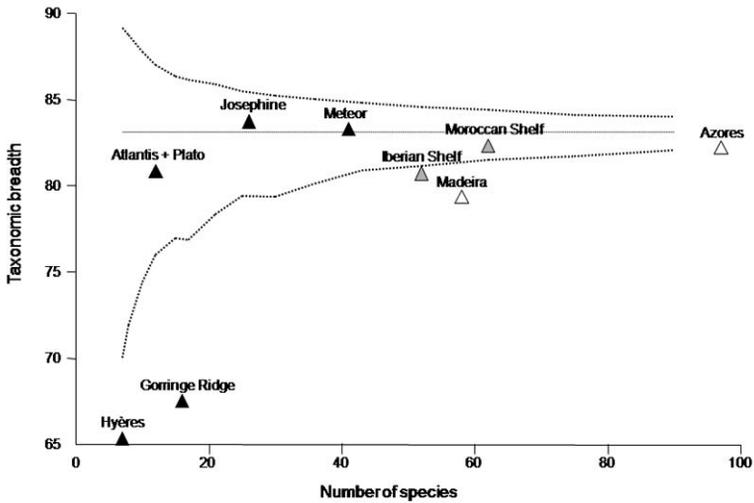


Figure 5. Funnel plot of taxonomic breadth ( $\Delta^+$ ) for deep-water coral assemblages at sites in the warm temperate NE Atlantic. Dotted lines indicate the 95% confidence intervals for taxonomic breadth at any given level of species richness (x-axis); sites lying below these bounds have lower taxonomic breadth than expected at their richness level given the taxonomic composition of the pool of species from which they are drawn. Seamounts—black symbols, Continental Shelf—grey symbols, Oceanic Islands—open symbols.

Large, deep-water coral reefs are afforded a degree of physical protection from bottom trawling due to the risks they pose to fishing gear (Hall-Spencer et al., 2002) which helps explain why live reefs can still be found along the coasts of Ireland (Grehan et al., 2004), Scotland (Roberts et al., 2005), and Norway (Fosså et al., 2005). However, the vast majority of deep-water coral species (e.g., many scleractinians and all stylasterids, antipatharians, zooanthids, and gorgonians) form more isolated colonies that are highly vulnerable to damage from rockhopper gear and reinforced sweeper nets. Unlike scleractinian reefs, these corals do not leave clear evidence of trawling damage so it is not possible to determine their historical distribution and abundance based on post-fishing surveys. The accumulation of historical information on deep-water habitats is time-consuming but can clearly provide a wealth of information to help our understanding of the ecology of the deep-sea biota and to inform policy influencing the management of remaining resources. Given that deep-water trawling is the major cause of damage to deep-water habitats, decisions over where to curb these activities must be underpinned by pooling data on the distributions of sensitive benthic species with data on the distribution of deep-water trawling to highlight areas where pristine habitats are likely to still be found.

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