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Diversity, distribution and spatial structure of the cold-water coral fauna of the Azores (NE Atlantic)

A. Braga-Henriques¹, F. M. Porteiro¹, P. A. Ribeiro¹, V. de Matos¹, I. Sampaio¹,
O. Ocaña², and R. S. Santos¹

¹Centre of IMAR of the University of the Azores, Department of Oceanography and Fisheries (DOP) and LARSyS Associated Laboratory, Rua Prof. Dr. Frederico Machado 4, 9901-862 Horta, Portugal

²Fundación Museo del Mar, Autoridad Portuaria de Ceuta, Muelle Cañonero, 51001, North Africa, Ceuta, Spain

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Correspondence to: A. Braga-Henriques (andreiahenriques@uac.pt)

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Abstract

Cold-water corals are widely considered as important structural components of benthic habitats, potentially enhancing local abundance in a variety of fish and invertebrate species. Yet, current knowledge of the taxonomic diversity and distribution patterns of these vulnerable, slow-growing organisms is scarce and fragmented, limiting the effectiveness of spatial management and conservation measures. We have conducted an exhaustive compilation of records of alcyonaceans, antipatharians, scleractinians and stylasterids available until the present day to assess the diversity, distribution, and spatial structure of coral assemblages in the Azores Exclusive Economic Zone (EEZ). The resulting database comprises 2501 entries concerning historical oceanographic expeditions and other published sources, as well as recent data from longline bycatch. Our taxonomic inventory appears to be fairly complete for the explored habitats, accounting for 164 species (79 alcyonaceans, 58 scleractinians, 18 antipatharians and 9 stylasterids), nine of which were new records. The Azores EEZ harbours a mixed coral fauna with several zoogeographic origins, showing the closest affinity with the Lusitanian–Mediterranean region. Very few apparent endemics were found (14 %), and only in part supported by consistent sampling. Coral diversity is particularly high between 300 and 900 m depths, in areas recognized as traditional fishing grounds or exploitable fish habitat within the 100-mile limit of the EEZ. The composition of coral assemblages shows significant geographical structure among longitudinal sections of the study area at comparable depths (100–1500 m). There is no evidence of a possible role of the Mid-Atlantic Ridge or latitudinal effects underlying this pattern, which suggests that it may instead reflect assemblage variability among features. Stronger changes in species composition were found along the bathymetric gradient. Notwithstanding the mix of partially overlapping steno- and eurybathic species that characterize the vertical distribution of corals, there is a distinct transition from shallow (100–600 m) to intermediate (600–1000 m) depths. The analysis here presented constitutes a valuable contribution

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1 Introduction

Cold-water corals are currently recognised as vulnerable and worth conserving due to 5 their slow growth (e.g. Sherwood and Edinger, 2009; Roark et al., 2009; Carreiro-Silva et al., 2012) and important role as structural elements that enhance habitat complexity and heterogeneity (FAO, 2009; Buhl-Mortensen et al., 2010; OSPAR, 2010; Auster et al., 2011). Widely distributed throughout the world's oceans, they can be found on 10 continental shelves and margins, edges and slopes of oceanic islands, seamounts, canyons and ridges (e.g. Cairns, 2007; Wareham and Edinger, 2007; Molodtsova et al., 2008; Mortensen et al., 2008; Reveillaud et al., 2008; Baker et al., 2012), especially in areas of high currents and/or enhanced suspended or re-suspended organic matter 15 (Davies et al., 2009; Guinan et al., 2009).

Occupying an area of almost one million km² on the Northeast Atlantic, the Exclusive 15 Economic Zone (EEZ) of the Azores archipelago comprises a rich submarine topography reaching 5000 m depths. Calculations based on bathymetry data identified the presence of 63 large and 398 small seamounts-like features in the area (Morato et al., 2008), thus making it suitable for corals.

Major oceanographic expeditions during the late nineteenth century and through- 20 out the 1900's (e.g. Josephine, Challenger, Talisman, campaigns of the Prince Albert I of Monaco, Biaçores, Bartlett) were a rich source of coral records. Until now, this information had been scattered through numerous reports and taxonomic publications lacking a common taxonomic nomenclature and often difficult to access. Hall-Spencer et al. (2007) launched an on-line database comprising part of the historical records 25 from Prince Albert I of Monaco and Biaçores campaigns regarding scleractinian, antipatharian and gorgonian taxa (exclusive of 5 families from the order Alcyonacea) found at depths > 200 m. For the Azores, only 46 taxa were included in the database.

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A synthesis of all key prior campaigns and other available information on past coral records, covering a broader taxonomic range is still lacking for the Azores. This step is essential to build a database that will enable investigating patterns of species distributions on a regional scale.

On-going efforts to map, describe and catalogue benthic communities of the Azores using video surveys are contributing to the discovery of coral gardens (Braga-Henriques et al., 2012; Tempera et al., 2012), providing inputs to the EUNIS European hierarchical biotope classification system (Galparsoro et al., 2012) and to OSPAR – Convention for the Protection of the Marine Environment of the Northeast Atlantic (OSPAR, 2010). However, this information is spatially restricted due to logistical constraints and the high costs associated with deep sampling. In comparison, the combination of historical records with data from fisheries by-catch and from occasional surveys can provide a more insightful picture of the diversity and distribution of corals in this region.

The main goal of this study is to assess the diversity, distribution and biogeographical patterns of corals belonging to orders Alcyonacea, Antipatharia and Scleractinia, and the hydrozoan family Stylasteridae in the Azores. Along with a brief account of historical coral collection in the region since the mid-nineteenth century, we present an updated taxonomic inventory based on historical sources and unpublished data collected by the Centre of IMAR and Department of Oceanography and Fisheries of the University of the Azores in recent years. Geo-referenced species records were used to map the distribution of the major taxonomic groups, and to estimate species richness at regional, local and bathymetric scales. Furthermore, we examined the spatial structure of coral assemblages by testing the hypotheses of no differences in the species lists among (1) feature types (island or seamount), (2) longitudinal sections of the EEZ and (3) depth intervals.

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2 Material and methods

2.1 Study area

The Azores EEZ is located in the NE Atlantic near the triple junction of the North American, Eurasian and African plates between 33° 46' N–42° 57' N, 35° 45' W–21° 05' W (Fig. 1). It comprises nine volcanic islands of recent origin (Azevedo et al., 1991) with narrow shelves and steep slopes, spread along a NW–SE-trending strip of 600-km long, with the Mid-Atlantic Ridge (MAR) separating the islands of Flores and Corvo, to the west, from the remaining island groups. Numerous seamounts of very different size, shape and depth are scattered throughout the study area (Morato et al., 2008).

Ocean circulation patterns in the Azores are complex (Santos et al., 1995; Alves and Verdière, 1999; Johnson and Stevenson, 2000). Large scale circulation is dominated by two eastward-flowing branches of the Gulf Stream, the cold North Atlantic Current (NAC) in the north, crossing the MAR between 45–48° N (Bower et al., 2002), and the warm Azores Current (AzC) in the south, which crosses the MAR between 34–36° N (Alves and Verdière, 1999). One additional eastward flow can be traced between the NAC and the AzC at 39–42° N (Reverdin et al., 2003). Mesoscale eddies also occur on both sides of the AzC (Alves and Verdière, 1999). The Azores is a transitional region between subtropical and temperate climate. Sea temperature is characterized by horizontal gradients enhanced by the NAC and the AzC flows (Bashmashnikov et al., 2004).

2.2 Review and compilation of coral data

Historical and new coral records included specimens of the anthozoan orders Alcyonacea, Antipatharia, Scleractinia and the hydrozoan family Stylasteridae, which are the most commonly recorded taxonomic groups in the Azores showing habitat-forming features. In the scope of this study, one record is the occurrence of one or more individuals of any give taxon at a specific location. We have conducted an exhaustive

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Zibrowius and Cairns, 1992). A small proportion of our classifications (*Dentomuricea aff. meteor*, *Leiopathes* sp. A, *Elatopathes* aff. *abietina*) should be considered tentative given that these taxa are still under review. The studied material is deposited in the reference collection of the IMAR-DOP/UAc (COLETA).

5 2.3 Data analysis

2.3.1 Distribution and species richness

Distribution maps were plotted based on all geo-referenced records available for each taxonomic group (Alcyonacea, Antipatharia, Scleractinia and Styelasteridae). To identify potential hotspots of coral diversity species richness was calculated in 20 × 20 km grid cells using XTools Pro 9.0 for ArcMap and R (R Development Core Team, 2011). The vertical distribution of individual species was also computed to assess bathymetric profiles of species richness for each taxonomic group and all groups combined. Species accumulation curves and 95 % confidence intervals based on incidence (presence-absence) of species by sample were estimated using the Mao Tau indicator of expected species richness in EstimateS 8.0 (Colwell, 2006). To minimize possible bias due to the inherent differences in sampled areas between gear types (Colwell et al., 2004), we calculated accumulation curves separately for trawled (trawls, dredges, etc.) and longline gears.

2.3.2 Spatial trends in assemblage composition

Geographical and bathymetric structure of coral assemblages was investigated using multivariate analysis with the software package PRIMER-E v.6.1.6 (Clarke and Gorley, 2006). Records were assigned to a specific geomorphic feature (oceanic island or seamount) whenever their position was on that feature (verified using GIS) or, if sampling coordinates were missing, when there was a specific mention to the feature name. Confirmation of seamount positions was based on Morato et al. (2008). The available

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were calculated using 5000 permutations. First we tested for differences among islands and seamounts by means of a two-way crossed ANOSIM of feature type against the combination of longitudinal section and depth interval to remove all effects of these two factors. Global R for feature type was not significant ($R = 0.153$, $P = 0.065$), so

- 5 a two-way crossed ANOSIM was performed to test for differences among longitudinal sections and depth intervals not considering feature type. To identify those taxa contributing the most to the observed dissimilarities among longitudinal sections and depth intervals we used similarity percentages (SIMPER) analysis following the ANOSIM design. Species were ranked according to their average contribution to the total between-group average dissimilarity and the ratio of average to standard deviation of their contribution, which is a useful measure for good discriminating species.
- 10

3 Results

3.1 Historical review

To our knowledge Verrill (1864) provided the first coral records from the Azores, namely

- 15 *Callogorgia verticillata*, *Viminella flagellum* and *Errina aspera* (although the latter was in fact *Errina dabneyi* according to Zibrowius and Cairns, 1992). Specimens were collected around Faial Island, most likely by local fisherman, and donated to the Museum of Comparative Zoology (Cambridge, USA) by Chas. Dabney.

- The number of records would greatly increase in the following decades as a result
20 of a period of heightened discovery in the deep-sea that runs from approximately 1855 to 1931, when major oceanographic expeditions conducted through the North Atlantic investigated the epibenthic fauna. The Josephine (1869), Challenger (1873) and Talisman (1883) were the first scientific expeditions sampling corals in the Azores. Ten and 11 species were documented from Josephine and Challenger, respectively. The highest coral richness was, however, obtained from the Talisman campaign, on which 14 species were collected from the 26 dredges made in the Azores at depths between 80
25

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Our final major source of historical occurrences was the CANCAP-V expedition with HNIMS *Tyde man* (May/June 1981), during which 192 bottom stations were sampled in the vicinity of the three island groups using gears such as Agassiz trawl, beam trawl, rectangular and triangular dredge, and Van Veen grab (Van der Land, 1987). We now report a coral collection deposited at the Naturalis Museum in Leiden of at least 144 specimens belonging to 10 different families. This collection contains 19 alcyonacean and 8 scleractinian species collected from 41 stations (55–3150 m). Additional records of antipatharians are also listed in the museum database of the Smithsonian National Museum of Natural History (<http://collections.si.edu/search/>), increasing the Cancap-V inventory to at least 32 coral species.

Since this campaign new species records were described *Scyphopodium ingolfi* (Bayer, 1981), *Azoriella bayeri* (López-González and Gili, 2001), *Alcyonium profundum* (Stokvis and Van Ofwegen, 2006), *Coralium niobe* (Sampaio et al., 2009) and *Antipathella subpinnata* (de Matos et al., 2012). Video surveys conducted in the Azores showed evidence of rich coral communities. Yet, these did not document new records nor described new species (e.g. Braga-Henriques et al., 2012; Tempera et al., 2012). In addition, observations with the submersible *Archimèd* in 1969 commonly refer to generalist names such as gorgonians or antipatharians and many recognized taxa are reported with question marks (CNEXO, 1972).

20 3.2 Taxonomy of new records

Of all the specimens examined, 1575 were identified to species level, 270 to genus level and 125 to family level. Alcyonaceans accounted for the majority of the individuals (56.6 %) followed by scleractinians (24.2 %), antipatharians (10.2 %) and stylasterids (9.0 %). Out of 157 species compiled from the literature, we identified 61 in the IMAR-DOP/UAc records. In addition, we now report nine new species records for the Azores: *Alcyonium maristenebrosi* (Alcyonacea: Alcyoniidae), *Alcyonium rubrum* (Alcyonacea: Alcyoniidae), *Paragorgia johnsoni* (Alcyonacea: Paragorgiidae), *D. aff. meteor* (Alcyonacea: Plexauridae), *Lepidisis cyanae* (Alcyonacea: Isididae),

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Leiopathes sp. A (Antipatharia: Leiopathidae), *Distichopathes* sp. (Antipatharia: Aphanipathidae), *Coenocyathus cylindricus* (Scleractinia: Caryophylliidae) and *Dendrophyllia ramea* (Scleractinia: Dendrophylliidae).

3.3 Distribution and species richness

- 5 The combination of historical and IMAR-DOP/UAc records resulted in a database containing 2501 entries, 88 % of which are geo-referenced and comprise 1128 records of Alcyonacea, 744 of Scleractinia, 185 of Styasteridae and 151 of Antipatharia. The updated inventory for the Azores EEZ now accounts for a total of 164 species, comprising 79 alcyonaceans (15 families), 18 antipatharians (5 families), 58 scleractinians (10 families) and 9 stylasterids (see Appendix A, Table A1). Approximately 30 % of the
10 species were represented by one or two records, while only 19 % of them contributed with 20 records or more (Fig. 2). The most common species by number of records were *V. flagellum* (120 records), *C. verticillata* (116), *D. aff. meteor* (106), *E. dabneyi* (85), *Caryophyllia (Caryophyllia) cyathus* (75), *Madrepora oculata* (72), *Acanthogorgia armata* (66) and *Lophelia pertusa* (64).

Despite the considerable discrepancy between taxonomic groups in the number of species and data points available, all groups showed a similar distribution pattern (Fig. 3). Corals were mostly found around islands and on nearby seamounts, especially those located southwest of Faial and south of São Miguel, with very few records
20 falling outside the 100-mile limit of the EEZ and the Azores plateau. Spatial patterns of species richness broadly reflect collection effort and revealed that areas of high taxonomic diversity (> 20 species) are found widespread throughout the archipelago (Fig. 4). By feature, species richness ranged from one species at several poorly-sampled seamounts to 73 species (157 records) at São Miguel island.

25 Species accumulation curves indicate that the regional coral fauna is relatively well sampled regardless of the type of gear used (Fig. 5). The curve corresponding to long-line data quickly reached a state of near-saturation, indicating that the addition of new species was slow after the most common ones had been sampled. In contrast, the

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curve calculated from trawled gear samples grew steeper, as a result of the greater area sampled per haul compared to longlines. Although an asymptote has not yet been reached in both cases, it is unlikely that further sampling of the habitats already surveyed will lead to the discovery of more than a few rare species.

- 5 The data set covered a broad bathymetric range (5–3215 m). Some species, such as *Acanella arbuscula* (815–3100 m) and *Solenosmilia variabilis* (424–2050 m), showed broad depth distributions, while others occurred within narrow depth ranges as was the case of the deep bathyal species *A. profundum* (2200–2600 m) and *Flabellum (Ulocyathus) angulare* (2085–2720 m) or *Paracalyptrophora josephinae* (200–624 m) and
10 *Dasmosmilia lymani* (142–230 m) at shallower depths (see Appendix A, Fig. A1 for individual depth ranges of all species).

The bulk of records were concentrated at upper bathyal depths, between 100–600 m, while the highest diversity occurred between 300 and 900 m depths, reaching its peak at 500–600 m with 59 species from all groups (Fig. 6). Maximum diversity occurred at
15 different depths for each group: 500–600 m for Alcyonacea (29 species); 400–500 m for Antipatharia (seven species); 500–600 m and 700–800 m for Scleractinia (24 species); 800–1000 m for Stylasteridae (six species). We found a marked decrease in species richness below 2200 m, which was coincident with a scarcity of records. Stylasterids were absent at these greater depths, and the other groups were represented by 10
20 alcyonacean, two antipatharian and four scleractinian species.

3.4 Multivariate analysis of community structure

Two-way crossed ANOSIM revealed statistically significant gradients in assemblage composition among longitudinal sections averaged across depth intervals (Global $R = 0.25$; $P = 0.000$) and among depth intervals averaged across longitudinal sections of the study area (Global $R = 0.41$; $P = 0.000$). Pairwise comparisons among levels for
25 each factor were all statistically significant (Table 4). The higher Global R value obtained for depth indicates that this effect had the strongest contribution to the overall trend. On the other hand, the existence of a longitudinal gradient should be interpreted

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4 Discussion

To our knowledge the data here presented constitute the most comprehensive biogeographical database yet created on a regional coral fauna of the Northeast Atlantic. Research conducted at IMAR-DOP/UAc since the mid-2000s using by-catch and occasional collection led to an almost twofold increment in the number of geo-referenced occurrences for corals, greatly increasing the spatial coverage of distributional data and the material available for taxonomic studies. Even though the newly collected specimens were largely assigned to species that had already been reported in the literature, their examination improved our knowledge of the coral diversity in the region, extending the known geographical distribution of nine species to the Azores. Judging from the species accumulation curves, the updated species inventory here presented seems fairly complete. Nonetheless, based on the poorer sampling of habitats deeper than 1500 m, this list is likely to grow with species typical of greater depths. Additionally, once the uncertain taxonomic status of a few specimens is clarified more species may be added. Coral taxonomy is complex, especially within certain groups for which some morphological descriptions lack sufficient clarity to distinguish between different states of a character, and others are based on limited material (e.g. *Sarcodictyon charcoti*, *Titanideum obscurum*, *Thesea rigida*) and may not cover the entire range of intraspecific morphological variability. The use of molecular tools may thus prove to be essential in assisting classical taxonomy in the discrimination between closely related species in these problematic groups (McFadden et al., 2011).

4.1 Species composition

Order Alcyonacea presented the highest diversity of species and number of records, suggesting that this is the dominant coral group in the Azores. However, we should consider the possibility of a negative sampling bias of solitary scleractinians in IMAR-DOP/UAc records. Historical surveys were mainly conducted with the use of trawled gears, whereas the recent records were based mostly on bottom longline. While the

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first are non-selective, the latter is less efficient for sampling solitary scleractinians than generally larger colonial species possessing more complex shapes (e.g. arborescent, bottlebrush, lyriform, reticulate). A recent four-month survey of the by-catch from commercial longline fishery based at Horta revealed that the most frequently landed taxa were *Leiopathes* spp., *E. dabneyi* and *Dendrophyllia* sp., all possessing three-dimensional branched shapes (Sampaio et al., 2012). In the same survey, solitary scleractinians were all collected as secondary by-catch. Thus, notwithstanding the inevitable geographical and vertical heterogeneity of sampling effort present in our data set, the relative proportions among taxa are likely to provide a good representation of the coral fauna in the Azores, perhaps with the exception of solitary scleractinians.

4.2 Species distribution and richness

The distribution of corals was mainly clustered around insular slopes and on the edges and peaks of seamounts, in particular those located south of Faial island (Açor, Princesa Alice and Condor de Terra) and south of São Miguel (Mar da Prata).

These findings are in line with the known habitat requirements for most coral species, namely the presence of hard substrates with high topographic relief (Genin et al., 1986; Mortensen and Buhl-Mortensen, 2004; Guinan et al., 2009; Tong et al., 2012), low levels of sedimentation (Roberts et al., 2006), enhanced current flow (Frederiksen et al., 1992; Mienis et al., 2007; Dorschel et al., 2007) and high food supply (Bryan and Metaxas, 2007; Davies et al., 2009).

Coral observations were strongly linked with traditional fishing grounds within the 100-mile EEZ. Maximum species richness was achieved within the exploitable fish habitat, which is restricted to depths < 600 m and corresponds to about 1 % of the EEZ (Menezes, 2003). Important areas for fisheries were identified as hotspots of coral diversity, such as the Açor (51 species recorded), Mar da Prata (41 species) and Princesa Alice (32 species) seamounts. Our observations are in agreement with previous studies suggesting an important role of cold-water coral communities as habitat providers for numerous fish and invertebrates (Husebø et al., 2002; Buhl-Mortensen

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et al., 2010; Söffker et al., 2011; Baillon et al., 2012; Braga-Henriques et al., 2012), favouring the aggregation of commercial species and increased local productivity. A full understanding of the degree of interaction between those communities and fisheries will require further studies combining coral distribution data and estimates of fishing effort for the region.

4.3 Endemism and zoogeographic affinities

Previous studies supported the proposition that isolation among seamounts promote high rates of speciation and endemism (Richer de Forges et al., 2000; Koslow et al., 2001; Stocks and Hart, 2007). This prediction is being currently challenged by increasing reports of seamount megafaunas characterized by species with broad geographical distributions and few endemics (e.g. Samadi et al., 2006; O'Hara, 2007; McClain et al., 2009), including coral assemblages in the North Atlantic (Cairns and Chapman, 2001; Thoma et al., 2009). Our study is in agreement with the latter given that the Azores region hosts a coral fauna of mixed zoogeographic affinities and only 23 of the 164 species (14 %) are apparent endemics (Table 5). It is, however, worth noting that only eight of these were consistently sampled throughout the study area (none were restricted to a unique feature), making conclusions regarding their regional endemicity more robust than for the remaining taxa, the vast majority of which were only recorded once. In the case of these rare species, it is for now impossible to tease apart potential endemicity from an artifact of undersampling with any degree of confidence. Increasing sampling areas will lead to an increased probability of encountering rare species (Gotelli and Colwell, 2001). Therefore further surveys of poorly explored areas in the North Atlantic will help clarify this issue. The uncertainty regarding endemicity is even greater for those groups that are less well studied (e.g. Clavulariidae, Nephtheidae and Anthothelidae) and thus likely under-represented in species lists worldwide due to limited taxonomic expertise.

The coral fauna of the Azores shows the closest affinity with the Lusitanian–Mediterranean zoogeographic region, with which it shares 71 % of its species. A similar

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cornuformis, *S. variabilis*, *F. alabastrum*, *F. angulare* and *Enallopsammia rostrata* (see Waller, 2005 and references therein), as well as the alcyonacean *A. arbuscula* (Beazley and Kenchington, 2012). This is likely the prevailing reproductive mode also in antipatharians in general (Wagner et al., 2012). For most of the above species a lecithotrophic larval stage was inferred from oocyte size and planulae observations. Development times (and therefore dispersal distances) are reportedly low for many shallow water lecithotrophic larvae (Shanks, 2009). In the deep-sea, however, the effects of low temperature (O'Connor et al., 2007; Bradbury et al., 2008) and pressure (Somero, 1998) on larval metabolism may extend planktonic larval duration leading to an increase of dispersal potential. In addition, some lecithotrophic coral larvae have the ability to delay metamorphosis for months, thus greatly prolonging the dispersive phase (Cordes et al., 2001; Sun et al., 2010).

A correspondence between low dispersal potential and narrow geographical range is apparent among the Stylasteridae. This family, generally reported as having brooded larvae with very short planktonic periods (Brooke and Stone, 2007), shows the highest rate of apparent endemism (four out of nine species) and limited distributions among the four major groups examined in this study. However, the same relationship was not observed in another brooding species, *Anthomastus grandiflorus* (Mercier and Hamel, 2011), which has a wide geographical distribution. It seems therefore clear that although larval type may largely determine dispersal potential, a number of other factors such as dispersal barriers, currents and larval behaviour, may come into play to modulate realized dispersal and limit range size (McClain and Hardy, 2010). Finally, a hypothetical role of asexual reproduction (budding, fission, parthenogenesis, etc.) especially for direct developing species cannot be ruled out, even though its effectiveness has not been assessed in deep-sea species.

4.4 Spatial structure

Our multivariate analysis revealed significant geographical structure in assemblage composition across the study area. Possible explanations for this result are unclear

owing to the fact that the observed pattern of differentiation among longitudinal sections was not supported by the presence of consistently discriminating species. It should be noted that, because only presence-absence data were used, hypothetical geographical patterns arising from changes in abundance or species dominance, not composition, remain undetected.

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The spatial structure in species composition found in our data may reflect variability among features, as suggested by data points in the nMDS ordination being loosely clustered. On the other hand, the placement of the study area along a 600-km NW–SE strip intersected by the MAR (which separates western from central and eastern sections), may help to explain the observed geographical differences if: (1) a higher proportion of western species or a lower proportion of eastern species was found on the western section, suggesting that the MAR could be an effective biogeographical barrier; (2) a higher proportion of northern species or a lower proportion of southern species was found in the western group compared to the central and especially the eastern group, indicating of a latitudinal effect. We classified each species in terms of latitudinal range (endemic, northern, southern, broadly distributed) and zoogeographic affinity (endemic, Great Meteor seamount, eastern, western, amphi-Atlantic, cosmopolitan) and tested if their relative proportions differed among longitudinal sections using separate chi-square tests. We found no significant differences, both for latitudinal range ($\chi^2 = 2.048$, $P = 0.915$, d.f. = 6) and zoogeographic affinity ($\chi^2 = 6.752$, $P = 0.749$, d.f. = 10).

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The above results suggest that the MAR does not constitute a biogeographic barrier for corals in the area. This is in line with previous surveys of deep-sea fauna at the MAR, which did not report any marked cross-ridge differences in species composition for bathypelagic (Sutton et al., 2008) and demersal fish (Bergstad et al., 2008). However, we cannot rule out the possibility that the MAR may pose an obstacle to east-west dispersal, especially in lower bathyal (Gebruk et al., 2010) and abyssal fauna (McClain et al., 2009b; Etter et al., 2011). The scarcity of records for these depths in our data set does not allow investigating this hypothesis.

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A latitudinal gradient in species composition was not observed at the spatial scale of this study. The northernmost and southernmost sampling locations, differing roughly by 2.5 degrees of latitude, showed similar proportions of northern vs. southern species. Such differences are likely to arise at wider latitudinal ranges. For example, a distinct latitudinal variation in the composition of demersal fish assemblages (e.g. Hareide and Garnes, 2001; Bergstad et al., 2008; Bergstad et al., 2012) and bathyal invertebrate fauna (Gebruk et al., 2010) was detected between different sections of the northern MAR, but not in demersal fishes within the Azores archipelago (Menezes et al., 2006). Recent surveys on the MAR north of the Azores revealed that most of the 5 alcyonaceans, antipatharians and scleractinians found are shared with the Azores (Molodtsova et al., 2008; Mortensen et al., 2008), but some of the few exceptions were species with northern or antitropical ranges, such as *Primnoa resedaeformis*, *Paragorgia arborea* and cf. *Bathyphathes arctica*. Latitudinal gradients in species distributions along the northern MAR and their underlying causes can only be fully understood with 10 more consistent sampling beyond the regional scale. Nevertheless, a faunal transition may occur (in particular above mid bathyal depths) in the vicinity of the northern boundary of the Azores EEZ, reflecting meridional temperature gradients established by the convergence of the major current flows in the region (Bashmashnikov et al., 2004).

The strongest changes in species composition occurred with depth. Depth-related 15 faunal zonation (e.g. Copley et al., 1996; Howell et al., 2002; Menezes et al., 2006; Yeh and Drazen, 2008; Bergstad et al., 2012) and even vertical stratification within the same species (Zardus et al., 2006; Miller et al., 2011) have been commonly reported in the deep-sea. The rate of faunal change assessed in this study was more pronounced from shallow (100–600 m) to intermediate (600–1000 m) depth intervals, possibly reflecting sharper environmental gradients but also greater topographic complexity and substrate heterogeneity usually found at upper bathyal depths (Buhl-Mortensen et al., 2010). The fact that soft substrates become predominant at greater depths and restrict 20 the establishment of corals requiring hard substrates to settle could also explain the

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sharp decrease in species diversity below 2200 m, although this observation should be considered cautiously due to the relatively limited sampling at those depths.

We did not identify clear faunal boundaries, but rather a mix of steno- and eurybathic species with partially overlapping distributions. As expected, this pattern suggests that 5 a combination of factors are involved in the establishment of depth ranges, such as food availability, temperature, pressure and stratification of water masses, as well as biological interactions and processes such as competition, predation and dispersal (re-reviewed by Carney, 2005). Moreover, our analysis did not account for bottom type, which means that there may be also a confounding effect of this variable, known to greatly 10 influence coral distribution (e.g. Baker et al., 2012), on the perceived vertical gradient of the coral fauna.

Two other depth-related trends of faunal change emerged from our data. First, the proportion of amphi-Atlantic and cosmopolitan species increased from 19 % and 16 %, respectively, at 100–600 m to 26 % and 23 % at the 1000–1500 m depth interval. This 15 observation agrees with the contention that species range sizes tend to increase with depth, possibly as a result of more constant environmental conditions (Etter and Rex, 1990; Allen and Sanders, 1996). Second, with increasing depth there was also a growing proportion of high-latitude species (7 % at 100–600 m to 21 % at 1000–1500 m) and a corresponding decline of low-latitude species (69 % at 100–600 m to 53 % at 1000– 20 1500 m). This pattern is consistent with the depth of the permanent thermocline in the NE Atlantic (600–1000 m) and the predominance beneath its lower boundary of deep-water masses formed at high latitudes (i.e. the Subarctic Intermediate Water and the Labrador Sea Water).

4.5 Conservation issues

25 Coral assemblages found on seamounts and island slopes showed high taxonomic richness at both species and family levels, indicating that benthic habitats of the Azores harbour numerous species currently recognized as key-indicators of vulnerable marine ecosystems – VMEs (OSPAR, 2008; FAO, 2009). The United Nations General

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More detailed spatial patterns may emerge as species lists are populated with new records, especially from deeper and less explored habitats (> 1500 m). However, standardized collection methods will be necessary to significantly improve the statistical power required to detect spatial changes in community structure by enabling the use of abundance data.

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One of the key aspects that must be considered in biogeographical studies of corals is the generally insufficient expertise in morphological taxonomy. This shortcoming may lead to inaccurate taxonomic inventories or to lists with low taxonomic resolution that will compromise the validity of assessed biogeographical patterns. Despite its growing usefulness, molecular systematics still requires integration with classic morphological taxonomy to achieve conclusive species identification. Therefore, a greater investment in taxonomic training will be essential to tackle the challenge of characterizing deep-sea faunas in a time of increasing, and more sophisticated, scientific exploration.

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Table 1. Data sources for the coral records obtained during the major oceanographic expeditions between 1869–1981 and other events with sporadic records. References herein were also used in the nomenclature revision.

Campaign	Year	Vessel/Vehicle	Sampling gear	Source
Josephine	1869	R/V <i>Josephine</i>	–	Lindström (1877), Aurivillius (1931), Zibrowius (1980), Bayer (1981)
Challenger	1873	HMS <i>Challenger</i>	Dredge, trawling	Moseley (1881), Studer (1889), Wright and Studer (1889), Zibrowius (1980)
Talisman	1883	R/V <i>Talisman</i>	Dredge	Gourret (1906), Hickson (1912), Boschma (1963), Zibrowius (1980), Grasshoff (1986), Zibrowius and Cairns (1992)
Campaigns of Prince Albert 1st of Monaco	1885–1888, 1895–1897, 1902–1905, 1911–1914	R/V <i>Hirondelle</i> , R/V <i>Princesse Alice</i> , R/V <i>Princesse Alice II</i> , R/V <i>Hirondelle II</i>	“Barre à fauberts”, double traps, trammel nets, traps, trawling	Studer (1890, 1891, 1901), Jourdan (1895), Roule (1902, 1905), Calvet (1903, 1911), Gravier (1915, 1920, 1921), Verrill (1922), Thomson (1927), Pax and Müller (1954), Grasshoff (1973, 1977, 1981, 1992), Zibrowius (1980), Carpine and Grasshoff (1985), Weinberg (1990), Zibrowius and Cairns (1992), Ocaña et al. (2000), Molodtsova (2006)
Biaçores	1971	R/V <i>Jean Charcot</i>	Dredge, epibenthic trawl, scuba diving	Tixier-Durivault and d'Hondt (1975), Grasshoff (1977, 1982), Zibrowius (1980), Zibrowius and Cairns (1992), Stokvis and Van Ovsegan (2006)
Bartlett	1975	USNS <i>Bartlett</i>	Dredge	Zibrowius (1980), Grasshoff (1981, 1982), Zibrowius and Cairns (1992)
CANCAP-V	1981	HNIMS <i>Tydemar</i>	Agassiz trawl, beam trawl, rectangular and triangular dredge, Van Veen grab	Collection information from Naturalis Museum Leiden and IMAR-DOP/University of the Azores, Collections of the Smithsonian National Museum of Natural History (http://collections.si.edu/search/), Grasshoff (1992)
Other	1864–2011	Submersibles <i>Archimède</i> (CNEXO), <i>Nautile</i> (IFREMER), <i>Lula</i> (FRN); ROVs <i>Luso</i> (EMEPC) and <i>SP</i> (DOP/UAc); commercial fishing vessels	Bottom longline, dredge, grabbing, scuba diving	Verrill (1864), Pourtalès (1871), CNEXO (1972), Zibrowius and Saldanha (1976), Zibrowius (1980), Bayer (1981), Carpine and Grasshoff (1985), Zibrowius and Cairns (1992), López-González and Gili (2001), Stokvis and Van Ovsegan (2006), Ocaña et al. (2007), Sampaio et al., (2009), Braga-Henriques et al. (2011), Carreiro-Silva et al. (2011), Braga-Henriques et al. (2012), Sampaio et al. (2012), Tempera et al. (2012), de Matos et al. (2012)

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[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)**Table 2.** Source details for coral IMAR-DOP/UAc records collected in the Azores EEZ.

Campaign	Date	Vessel	Gear	No. of individuals
ARQDAÇO	1995	R/V Arquipélago	Bottom longline	473
	2004–2005			
	2007–2008			
	2010–2011			
ASIMOV	2000	R/V Águas Vivas	Scuba diving	1
Bancos	2007	R/V Arquipélago	Scuba diving	4
BIO-FAPI 3	2003	R/V Arquipélago	Dredge	1
<i>Chaceon affinis</i>	2003	FV Garcia Miguel	Baited traps	10
CONDOR	2009–2010	R/V Arquipélago	Bottom longline, traps	171
CoralFISH/EMEPC/Açores	2010	NRP Almirante Gago Coutinho	ROV Luso	20
CoralFISH/Faial-Pico-Channel	2011	R/V Águas Vivas	ROV SP	4
CoralFishID	2010–2011	R/V Arquipélago	Bottom longline	130
CORAZON	2009	Ada Rebikoff	Submersible Lula	7
DEECON	2007	R/V Arquipélago	Bottom longline	15
Defending our Oceans/Greenpeace	2006	MV Esperanza	Towed-camera	9
EMAM/PEPC_M@rBis	2011	NTM Creoula	Scuba diving	2
EMEPC/LUSO/Açores	2009	NRP Almirante Gago Coutinho	ROV Luso	1
EMEPC/LUSO/Açores G3	2008	NRP Almirante Gago Coutinho	ROV Luso	11
EMPAFISH	2005	R/V Arquipélago	Bottom longline	3
FAIVI/IOTZ	2011	R/V L'Atalante	-	28
FISHOR	2002	FV Pakura	Bottom longline	19
LusoExpedição	2007	NTM Creoula	Scuba diving	17
MARPROF-Crustaço	2009–2011	R/V Arquipélago	Traps	13
METEOR-58/3	2003	R/V Meteor	ROV Quest	2
Observers	1980, 1982, 1990, 2002–2011	Commercial fishing vessels	Bottom longline, handline	1030
PESCPROF	2004–2005	R/V Arquipélago	Bottom longline	13
SEAHMA	2002	R/V L'Atalante	ROV Victor	1
Other	-	-	-	81

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Table 4. Results of the 2-way crossed ANOSIM test based on similarity matrix derived from presence/absence data. (a) Global tests on the effect of longitudinal section and depth interval; (b) Pairwise tests averaged across all section groups and across all depth groups. All results are significant ($P \leq 0.05$).

(a) Source of variation					
Longitudinal section		Depth interval			
Global <i>R</i>	<i>P</i>	Global <i>R</i>	<i>P</i>		
0.253	0.000	0.432	0.000		
(b) Source of variation					
Longitudinal section					
Western vs. Central		Western vs. Eastern		Central vs. Eastern	
<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>
0.270	0.003	0.201	0.039	0.263	0.006
Depth interval					
Shallow vs. Intermediate		Shallow vs. Deep		Intermediate vs. Deep	
<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>
0.506	0.000	0.549	0.000	0.166	0.007

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Table 5. Zoogeographic affinities of the coral fauna of the Azores EEZ. Values represent the percentage of faunal composition shared with each geographical region (in brackets is the percentage of species only found in that region, besides the Azores). Regions are adapted from Cairns and Chapman (2001) and Watling et al. (2011): IA–ID – Western North Atlantic, Cape Hatteras to Florida Straits, Antilles, Caribbean, Gulf of Mexico, Guyana to Tropical coast Brazil; IIA – Western North Atlantic, southern Greenland, East Canada from Baffin Island and Davis Strait to Cape Hatteras; IIB – Boreal Eastern Atlantic; IIIA – Lusitanian–Mediterranean; IIIB – Seamounts south of the Azores and between Portugal and Madeira; IIIC – West Africa, Mauritania, Senegal and Gulf of Guinea; IIID – Canary Islands and Cape Verde; IO – Indian Ocean; IWP – Indo-West Pacific; NEP – Eastern North Pacific. Data sources used to compile species distributions are listed in Table 1.

Taxonomic group	Western North Atlantic				Eastern North Atlantic				Outside NE Atlantic		Amphi-Atlantic	Potential endemic
	IA-ID	IIA	IIB	IIIA	IIIB	IIIC	IIID	IO	IWP	NEP		
Alcyonacea	10.37 (1.22)	4.27 (0.00)	9.76 (1.22)	33.54 (9.76)	7.93 (0.61)	14.63 (0.00)	14.02 (1.22)	3.05 (0.00)	0.61 (0.00)	1.83 (0.61)	12.20	7.93
Antipatharia	0.00	1.22	1.83	6.71	4.27	0.00	4.27	0.00	1.22	0.00	1.22	1.83
Scleractinia	19.51 (2.44)	10.98 (0.00)	7.93 (0.00)	29.27 (0.61)	15.85 (0.61)	9.76 (0.61)	10.98 (0.00)	0.00	9.76 (0.00)	0.00	21.95	1.83
Styleridae	1.22 (1.22)	0.00	0.00	1.83	0.61	0.00	1.22	0.00	0.00	0.00	0.00	2.44
All groups	31.10 (4.88)	16.46 (0.00)	19.51 (1.22)	71.34 (11.59)	28.66 (1.83)	24.39 (0.61)	30.49 (2.44)	3.05 (0.00)	11.59 (0.00)	1.83 (0.61)	35.37	14.02

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Table A1. List of species of Alcyonacea, Antipatharia, Scleractinia and Stylasteridae identified in the Azores EEZ according to major oceanographic campaigns, other sources and IMAR-DOP/UAc records. Records from the CANCAP-V available on-line at the collection database of the Smithsonian National Museum of Natural History are indicated with an asterisk. See Table 1 for data source details. Signs in boldface indicate new species records.

Taxa	Josephine	Challenger	Talisman	PAM	Biaçores	Bartlett	Cancap-V	Other	IMAR-DOP records
Alcyonacea									
“True soft corals”									
Cornulariidae									
<i>Cornulariidae cornucopiae</i> (Pallas, 1766)					+				
Clavulariidae									
<i>Azoriella bayeri</i> (López-González and Gili, 2001)							+		
<i>Bathyteleso rigida</i> (Wright and Studer, 1889)	+								
<i>Clavularia arctica</i> (Sars, 1860)					+				
<i>Clavularia armata</i> (Thomson, 1927)				+	+				
<i>Clavularia elongata</i> (Wright and Studer, 1889)	+				+		+		
<i>Clavularia marioni</i> (von Koch, 1891)				+	+				
<i>Clavularia tenuis</i> (Tixier-Durivault and d'Hondt, 1975)					+				
<i>Clavularia tubaria</i> (Wright and Studer, 1889)				+					
<i>Rolandia coralloides</i> (Lacaze-Duthiers, 1900)				+					
<i>Sarcodictyon catenatum</i> (Forbes, 1847)					+		+		
<i>Sarcodictyon charcoti</i> (Tixier-Durivault and d'Hondt, 1975)					+				
<i>Schizophytum echinatum</i> (Studer, 1891)				+	+	+	+		
<i>Scleranthelia rugosa</i> (Pourtales, 1867)	+								
<i>Scyphopodium ingolfi</i> (Madsen, 1944)							+		
<i>Telestula batoni</i> (Weinberg, 1990)					+				
<i>Telestula humilis</i> (Thomson, 1927)					+				
<i>Telestula kuekenthali</i> (Weinberg, 1990)					+				
Paralcyoniidae									
<i>Paralcyonium spinulosum</i> (Delle Chiaje, 1822)					+				

Table A1. Continued.

Taxa	Josephine	Challenger	Talisman	PAM	Biaçores	Bartlett	Cancap-V	Other	IMAR-DOP records
Alcyoniidae									
<i>Alcyonium bocagei</i> (Saville Kent, 1870)				+				+	
<i>Alcyonium grandiflorum</i> (Tixier-Durivault and d'Hondt, 1975)				+					
<i>Alcyonium maristenebrosi</i> (Stiasny, 1937)								+	
<i>Alcyonium palmatum</i> (Pallas, 1766)				+					
<i>Alcyonium profundum</i> (Stokvis and Van Ofwegen, 2006)							+		
<i>Alcyonium rubrum</i> (Stokvis and Van Ofwegen, 2006)								+	
<i>Anthomastus agaricus</i> (Studer, 1891)				+	+			+	
<i>Anthomastus canariensis</i> (Wright and Studer, 1889)					+				
<i>Anthomastus grandiflorus</i> (Verrill, 1878)					+		+		
<i>Bellonella bocagei</i> (Saville Kent, 1870)	+		+	+					
<i>Bellonella tenuis</i> (Tixier-Durivault and d'Hondt, 1975)					+				
<i>Bellonella variabilis</i> (Studer, 1891)				+	+				
<i>Pseudoanthomastus inusitatus</i> (Tixier-Durivault and d'Hondt, 1975)					+			+	
Nephtheidae									
<i>Gersemia clavata</i> (Danielssen, 1887)				+			+		
<i>Scleronephthya macrospina</i> (Thomson, 1927)				+					
Gorgonians "Scleraxonida"									
Anthothelidae									
<i>Anthothela grandiflora</i> (Sars, 1856)				+		+	+		
<i>Titanideum obscurum</i> (Thomson, 1927)				+					
Paragorgiidae									
<i>Paragorgia johnsoni</i> (Gray, 1862)							+		
Coralliidae									
<i>Corallium johnsoni</i> (Gray, 1860)				+		+	+		
<i>Corallium nobile</i> (Bayer, 1964)							+		
Gorgonians "Holaxonida"									

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Table A1. Continued.

Taxa	Josephine Challenger	Talisman	PAM	Biaçores	Bartlett	Cancap-V	Other	IMAR-DOP records
Acanthogorgiidae								
<i>Acanthogorgia armata</i> (Verrill, 1878)	+	+	+	+	+	+		
<i>Acanthogorgia aspera</i> (Pourtalès, 1867)			+					
<i>Acanthogorgia hirsuta</i> (Gray, 1857)	+	+		+	+	+		
<i>Acanthogorgia muricata</i> (Verrill, 1883)			+					
<i>Acanthogorgia pico</i> (Grasshoff, 1973)			+					
Plexauridae								
<i>Bebrype mollis</i> (Philippi, 1842)	+	+		+	+	+		
<i>Dentomuricea aff. meteor</i> (Grasshoff, 1977)						+		
<i>Muriceides lepida</i> (Carpine and Grasshoff, 1975)				+	+			
<i>Muriceides paucituberculata</i> (Marion, 1882)	+	+	+			+		
<i>Paramuricea candida</i> (Grasshoff, 1977)			+	+	+	+		
<i>Placogorgia beccana</i> (Grasshoff, 1977)		+						
<i>Placogorgia coronata</i> (Carpine and Grasshoff, 1975)				+				
<i>Placogorgia intermedia</i> (Thomson, 1927)	+	+		+	+			
<i>Placogorgia terceira</i> (Grasshoff, 1977)	+		+			+		
<i>Swiftia dubia</i> (Thomson, 1929)	+	+	+	+	+	+		
<i>Thesea rigida</i> (Thomson, 1927)		+						
<i>Villogorgia bebrycoides</i> (Koch, 1887)	+	+		+		+		
Gorgoniidae								
<i>Eunicella modesta</i> (Verrill, 1883)	+	+	+					
Gorgonians "Calcxonia"								
Chrysogorgiidae								
<i>Chrysogorgia agassizii</i> (Verrill, 1883)	+		+	+		+		
<i>Chrysogorgia elegans</i> (Verrill, 1883)		+						
<i>Chrysogorgia fewkesii</i> (Verrill, 1883) ^a		+						
<i>Chrysogorgia quadruplex</i> (Thomson, 1927)	+		+			+		
<i>Chrysogorgia squamata</i> (Verrill, 1883) ^b			+					
<i>Iridogorgia pourtalesii</i> (Verrill, 1883)		+						
<i>Metallogorgia melanotrichos</i> (Wright and Studer, 1889)	+			+		+		
<i>Radicipes fragilis</i> (Wright and Studer, 1889)		+				+		

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Table A1. Continued.

Taxa	Josephine	Challenger	Talisman	PAM	Biaçores	Bartlett	Cancap-V	Other	IMAR-DOP records
Ellisellidae									
<i>Nicella granifera</i> (Kölliker, 1865)	+	+				+	+		
<i>Viminella flagellum</i> (Johnson, 1863)	+	+	+	+	+	+	+		
Primnoidae									
<i>Callogorgia verticillata</i> (Pallas, 1766)	+	+				+	+		
<i>Candidella imbricata</i> (Johnson, 1862)	+	+	+			+	+		
<i>Narella bellissima</i> (Kükenthal, 1915)	+	+							
<i>Narella versluysi</i> (Hickson, 1909)	+						+		
<i>Paracalyptrophora josephinae</i> (Lindström, 1877)	+					+	+		
<i>Thouarella (Euthouarella) grasshoffi</i> (Cairns, 2006)	+	+							
<i>Thouarella (Thouarella) variabilis</i> (Wright and Studer, 1889)	+	+							
Isididae									
<i>Acanella arbuscula</i> (Johnson, 1862)	+	+	+	+	+		+		
<i>Chelidonisis aurantiaca</i> (Studer, 1890)	+	+							
<i>Isidella longiflora</i> (Verrill, 1883)				+	+		+		
<i>Keratoisis grayi</i> (Wright, 1869)	+	+				+	+		
<i>Lepidisis cyanae</i> (Grasshoff, 1986)					+				
Antipatharia									
Antipathidae									
<i>Antipathes erinaceus</i> (Roule, 1905)			+				+		
<i>Antipathes grayi</i> (Roule, 1905)		+							
<i>Antipathes virgata</i> (Esper, 1788)			+						
<i>Stichopathes dissimilis</i> (Roule, 1902)			+						
<i>Stichopathes flagellum</i> (Roule, 1902)			+						
<i>Stichopathes gravieri</i> (Molodtsova, 2006)			+			+	+		
<i>Stichopathes richardi</i> (Roule, 1902)			+						

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Table A1. Continued.

Taxa	Josephine	Challenger	Taliesman	PAM	Biaçores	Bartlett	Cancap-V	Other	IMAR-DOP records
Myriopathidae									
<i>Antipathella subpinnata</i> (Ellis and Solander, 1786)								+	+
<i>Antipathella wollastoni</i> (Gray, 1857)	+							+	
<i>Tanacetipathes squamosa</i> (Koch, 1886)	+								
Leiopathidae									
<i>Leiopathes glaberrima</i> (Esper, 1788)*						+	+		
<i>Leiopathes grimaldii</i> (Roule, 1902)	+					+	+		
<i>Leiopathes</i> sp. A							+		
Aphanipathidae									
<i>Distichopathes</i> sp.*					+				
<i>Elatopathes</i> aff. <i>abietina</i> (Pourtales, 1874)* ^c	+				+		+		
Schizopathidae									
<i>Bathyphates patula</i> (Brook, 1889)	+								
<i>Parantipathes hirondelle</i> (Molodtsova, 2006)	+						+		
<i>Stauropathes punctata</i> (Roule, 1905)*	+				+				
Scleractinia									
Pocilloporidae									
<i>Madracis pharensis</i> (Heller, 1868)							+	+	+
<i>Madracis profunda</i> (Zibrowius, 1980)					+				
Fungiacyathidae									
<i>Fungiacyathus</i> (<i>Bathyactis</i>) <i>crispus</i> (Pourtales, 1871)	+				+				
<i>Fungiacyathus</i> (<i>Bathyactis</i>) <i>marenzelleri</i> (Vaughan, 1906)					+	+	+		
<i>Fungiacyathus</i> (<i>Bathyactis</i>) <i>symmetricus</i> (Pourtales, 1871)	+				+	+			
<i>Fungiacyathus</i> (<i>Fungiacyathus</i>) <i>fragilis</i> (G. O. Sars, 1872)					+	+			

Table A1. Continued.

Taxa	Josephine	Challenger	Talisman	PAM	Biaores	Bartlett	Cancap-V	Other	IMAR-DOP records
Oculinidae									
<i>Madrepora oculata</i> (Linnaeus, 1758)		+	+	+	+		+	+	
Caryophylliidae									
<i>Anomocora fecunda</i> (Pourtalès, 1871)					+				+
<i>Aulocyathus atlanticus</i> (Zibrowius, 1980)				+	+				
<i>Caryophyllia (Caryophyllia) abyssorum</i> (Duncan, 1873)				+	+				+
<i>Caryophyllia (Caryophyllia) alberti</i> (Zibrowius, 1980)		+	+	+	+	+	+	+	
<i>Caryophyllia (Caryophyllia) ambrosia</i> (Alcock, 1898)		+	+	+	+	+	+	+	
<i>Caryophyllia (Caryophyllia) atlantica</i> (Duncan, 1873)		+	+	+	+	+	+	+	
<i>Caryophyllia (Caryophyllia) calveri</i> (Duncan, 1873)					+				
<i>Caryophyllia (Caryophyllia) cyathus</i> (Ellis and Solander, 1786)					+				
<i>Caryophyllia (Caryophyllia) foresti</i> (Zibrowius, 1980)					+				+
<i>Caryophyllia (Caryophyllia) inornata</i> (Duncan, 1878)					+				+
<i>Caryophyllia (Caryophyllia) sarsiae</i> (Zibrowius, 1974)					+				+
<i>Caryophyllia (Caryophyllia) smithii</i> (Stokes and Broderip, 1828)	+			+	+			+	+
<i>Coenocyathus cylindricus</i> (Milne Edwards and Haime, 1848)					+				+
<i>Concentrotheca laevigata</i> (Pourtalès, 1871)						+			
<i>Dasmosmilia lymani</i> (Pourtalès, 1871)						+			
<i>Dasmosmilia variegata</i> (Pourtales, 1871)					+	+			
<i>Deltocyathus eccentricus</i> (Cairns, 1979)					+	+	+		
<i>Deltocyathus italicus</i> (Michelotti, 1838)		+	+		+	+			
<i>Deltocyathus moseleyi</i> (Cairns, 1979)		+	+	+	+	+			
<i>Desmophyllum dianthus</i> (Esper, 1794)					+	+	+	+	+
<i>Lophelia pertusa</i> (Linnaeus, 1758)			+	+	+			+	+
<i>Paracyathus pulchellus</i> (Philippi, 1842)	+	+		+	+			+	+
<i>Pourtalosmilia anthophyllites</i> (Ellis and Solander, 1786)					+				
<i>Premocyathus cornuformis</i> (Pourtalès, 1868)					+	+	+	+	+
<i>Solenosmilia variabilis</i> (Duncan, 1873)					+	+	+	+	+
<i>Stephanocyathus (Odontocyathus) nobilis</i> (Moseley in Thompson, 1873)		+			+	+	+		
<i>Stephanocyathus (Stephanocyathus) crassus</i> (Jourdan, 1895)		+			+	+			
<i>Stephanocyathus (Stephanocyathus) diadema</i> (Moseley, 1876)		+			+	+			
<i>Stephanocyathus (Stephanocyathus) moseleyanus</i> (Sclater, 1886)					+	+	+	+	
<i>Tethocyathus variabilis</i> (Cairns, 1979)						+			
<i>Trochocyathus (Trochocyathus) spinosostatus</i> (Zibrowius, 1980)						+			
<i>Vaughanella concinna</i> (Gravier, 1915)					+	+	+		

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Taxa	Josephine	Challenger	Talismán	PAM	Biacôres	Bartlett	Cancap-V	Other	IMAR-DOP records
Turbinoliidae									
<i>Deltocyathoides stimpsonii</i> (Pourtales, 1871)	+			+	+				
<i>Peponocyathus folliculus</i> (Pourtales, 1868)	+			+	+				
<i>Sphenotrochus (Sphenotrochus) andrewianus</i> (Milne Edwards and Haime, 1848)	+				+				
Flabellidae									
<i>Flabellum (Flabellum) chunii</i> (Marenzeller, 1904)				+	+	+			+
<i>Flabellum (Ulocyathus) alabastrum</i> (Moseley in Thomson, 1873)	+	+	+	+	+	+			
<i>Flabellum (Ulocyathus) angulare</i> (Moseley, 1876)					+				
<i>Flabellum (Ulocyathus) macandrewi</i> (Gray, 1849)	+				+				
<i>Javania cailleti</i> (Duchassaing and Michelotti, 1864)				+	+				+
<i>Javania pseudoalabastra</i> (Zibrowius, 1974)				+	+				
Guyniidae									
<i>Guynia annulata</i> (Duncan, 1872)					+				
Stenocyathidae									
<i>Stenocyathus vermiciformis</i> (Pourtales, 1868)	+		+	+	+				+
Schizocyathidae									
<i>Schizocyathus fissilis</i> (Pourtales, 1874)				+	+				
Dendrophylliidae									
<i>Balanophyllia (Balanophyllia) cellulosa</i> (Duncan, 1873)					+				
<i>Dendrophyllia alternata</i> (Pourtales, 1880)					+				
<i>Dendrophyllia cornigera</i> (Lamarck, 1816) ^d					+		+	+	
<i>Dendrophyllia ramea</i> (Linneus, 1758)								+	
<i>Enallopsammia pusilla</i> (Alcock, 1902)					+				
<i>Enallopsammia rostrata</i> (Pourtales, 1878)			+	+	+		+	+	
<i>Leptopsammia formosa</i> (Gravier, 1915) ^e			+	+	+		+	+	

Table A1. Continued.

Taxa	Josephine	Challenger	Talismán	PAM	Biaçores	Bartlett	Cancap-V	Other	IMAR-DOP records
Athecatae									
Stylersteridae									
<i>Cryptelia affinis</i> (Moseley, 1879)	+	+					+		
<i>Cryptelia medioatlantica</i> (Zibrowius and Cairns, 1992)	+			+					
<i>Cryptelia tenuiseptata</i> (Cairns, 1986)	+	+	+				+		
<i>Cryptelia vascomarquesi</i> (Zibrowius and Cairns, 1992)	+	+	+						
<i>Errina atlantica</i> (Hickson, 1912)	+		+				+	+	
<i>Errina dabneyi</i> (Pourtalès, 1871)	+	+	+	+			+	+	
<i>Lepidopora eburnea</i> (Calvet, 1903)	+	+	+	+					
<i>Pliobothrus symmetricus</i> (Pourtalès, 1868)	+	+	+				+	+	
<i>Stenohelia</i> sp.A				+					

^a Even though Carpine and Grasshoff (1985) synonymized *Chrysogorgia fewkesii* from PAM with the species *Chrysogorgia quadruplex*, Cairns (2001) did not consider as valid the few records of *C. fewkesii* reported from the eastern Atlantic (PAM – Thomson, 1927; Biaçores – Tixier-Durivault and d'Hondt, 1975) given that they were based on fragmentary specimens or poorly described and there are slight differences among the chrysogorgiid species. However, we decided not to exclude the Biaçores record before original material could be examined;

^b The presence of *Chrysogorgia squamata* in the Azores is also doubtful (based in a single record), further examination of the original material is still required;

^c Specimens from two PAM stations are originally described as *Tanacetipathes squamosa*, but after the examination of the material at the Oceanographic Museum of Monaco we do believe that it is a misidentification (V. de Matos, personal communication, 2009);

^d Some of this material is still under revision given that we have found colonies showing different septa disposition when compared with the original description of *Dendrophyllia cornigera*;

^e Squires (1959) report this species to the Great Meteor and Atlantis seamounts, but Zibrowius did not examine these specimens (Zibrowius, 1980), and questioned the validity of those records. We followed his view and therefore considered *Leptopsammia formosa* as a putative endemic to the Azores.

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Longitudinal section				
	Av. Abund. Western	Av. Abund. Central	Diss/ SD	Contrib. (%)
Western vs. Central				
<i>Madrepora oculata</i>	0.23	0.59	0.69	4.86
<i>Desmophyllum dianthus</i>	0.23	0.48	0.69	3.76
<i>Stenocyathus vermiciformis</i>	0.46	0.19	0.62	3.18
<i>Pliobothrus symmetricus</i>	0.08	0.22	0.42	2.68
<i>Lophelia pertusa</i>	0.31	0.37	0.52	2.59
<i>Solenosmilia variabilis</i>	0.31	0.22	0.59	2.49
<i>Candidella imbricata</i>	0.15	0.33	0.58	2.49
<i>Acanthogorgia armata</i>	0.31	0.37	0.72	2.29
<i>Muriceides paucituberculata</i>	0.46	0.26	0.79	2.09
<i>Errina dabneyi</i>	0.15	0.41	0.64	2.04
<i>Swiftia dubia</i>	0.23	0.22	0.78	2.00
Western vs. Eastern	Av. Abund. Western	Av. Abund. Eastern	Diss/ SD	Contrib. (%)
<i>Pliobothrus symmetricus</i>	0.08	0.50	0.59	3.99
<i>Leptosammia formosa</i>	0.00	0.67	1.25	3.09
<i>Madrepora oculata</i>	0.23	0.42	0.52	2.97
<i>Muriceides paucituberculata</i>	0.46	0.42	0.82	2.65
<i>Lophelia pertusa</i>	0.31	0.33	0.85	2.21
<i>Acanella arbustula</i>	0.00	0.33	0.39	2.17
<i>Deltocyathus moseleyi</i>	0.15	0.42	0.81	2.15
<i>Stenocyathus vermiciformis</i>	0.46	0.17	0.79	2.11
<i>Errina atlantica</i>	0.08	0.42	0.64	2.04
<i>Flabellum alabastrum</i>	0.15	0.08	0.29	2.01
<i>Acanthogorgia armata</i>	0.31	0.33	0.67	1.96
<i>Eunicella modesta</i>	0.08	0.25	0.35	1.93
<i>Anthomastus agaricus</i>	0.15	0.33	0.78	1.84
Central vs. Eastern	Av. Abund. Central	Av. Abund. Eastern	Diss/ SD	Contrib. (%)
<i>Madrepora oculata</i>	0.59	0.42	0.54	3.85
<i>Desmophyllum dianthus</i>	0.48	0.33	0.57	3.63
<i>Acanella arbustula</i>	0.15	0.33	0.39	2.62
<i>Swiftia dubia</i>	0.22	0.33	0.89	2.59
<i>Caryophyllia sarsiae</i>	0.11	0.17	0.30	2.57
<i>Muriceides paucituberculata</i>	0.26	0.42	0.75	2.52
<i>Leptosammia formosa</i>	0.19	0.67	0.98	2.40
<i>Stephanocyathus moseleyanus</i>	0.15	0.08	0.28	2.34
<i>Errina atlantica</i>	0.19	0.42	0.68	2.30
<i>Lophelia pertusa</i>	0.37	0.33	0.78	2.30
<i>Candidella imbricata</i>	0.33	0.17	0.48	2.22
<i>Solenosmilia variabilis</i>	0.22	0.17	0.47	1.90

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Table A2. Continued.

Depth interval					
Shallow vs. Intermediate	Av. Abund. Shallow	Av. Abund. Intermediate	Diss/ SD	Contrib. (%)	
<i>Caryophyllia cyathus</i> *	0.78	0.11	1.41	3.47	
<i>Viminella flagellum</i>	0.83	0.28	1.14	3.20	
<i>Bebryce mollis</i>	0.67	0.06	1.28	2.96	
<i>Acanthogorgia armata</i>	0.61	0.17	1.08	2.88	
<i>Lophelia pertusa</i>	0.17	0.56	0.92	2.87	
<i>Callogorgia verticillata</i>	0.78	0.28	1.01	2.83	
<i>Acanthogorgia hirsuta</i>	0.50	0.11	1.02	2.62	
<i>Caryophyllia alberti</i>	0.56	0.11	0.73	2.60	
<i>Villogorgia bebrycoides</i>	0.56	0.11	0.93	2.57	
<i>Schizoplytum echinatum</i>	0.56	0.06	1.02	2.56	
<i>Desmophyllum dianthus</i>	0.39	0.39	0.69	2.50	
Shallow vs. Deep	Av. Abund. Shallow	Av. Abund. Deep	Diss/ SD	Contrib. (%)	
<i>Caryophyllia cyathus</i> *	0.78	0.00	1.64	3.75	
<i>Viminella flagellum</i> *	0.83	0.06	1.49	3.67	
<i>Callogorgia verticillata</i> *	0.78	0.00	1.44	3.54	
<i>Acanthogorgia armata</i>	0.61	0.25	0.91	3.00	
<i>Schizoplytum echinatum</i>	0.56	0.00	1.18	2.94	
<i>Caryophyllia alberti</i>	0.56	0.00	0.71	2.65	
<i>Bebryce mollis</i>	0.67	0.13	1.10	2.59	
<i>Desmophyllum dianthus</i>	0.39	0.38	0.66	2.58	
<i>Errina dabneyi</i>	0.50	0.06	0.91	2.57	
<i>Villogorgia bebrycoides</i>	0.56	0.00	0.97	2.46	
<i>Acanthogorgia hirsuta</i>	0.50	0.06	0.91	2.42	
Intermediate vs. Deep	Av. Abund. Intermediate	Av. Abund. Deep	Diss/ SD	Contrib. (%)	
<i>Madrepora oculata</i>	0.61	0.50	0.65	4.65	
<i>Lophelia pertusa</i>	0.56	0.31	0.83	4.28	
<i>Desmophyllum dianthus</i>	0.39	0.38	0.63	3.57	
<i>Stephanocyathus moseleyanus</i>	0.00	0.38	0.48	3.42	
<i>Pliobothrus symmetricus</i>	0.33	0.13	0.61	3.01	
<i>Solenosmilia variabilis</i>	0.28	0.31	0.67	3.01	
<i>Candidella imbricata</i>	0.22	0.31	0.63	2.93	
<i>Acanella arbuscula</i>	0.06	0.44	0.72	2.31	
<i>Callogorgia verticillata</i>	0.28	0.00	0.57	2.21	
<i>Chrysogorgia agassizii</i>	0.11	0.13	0.48	2.19	

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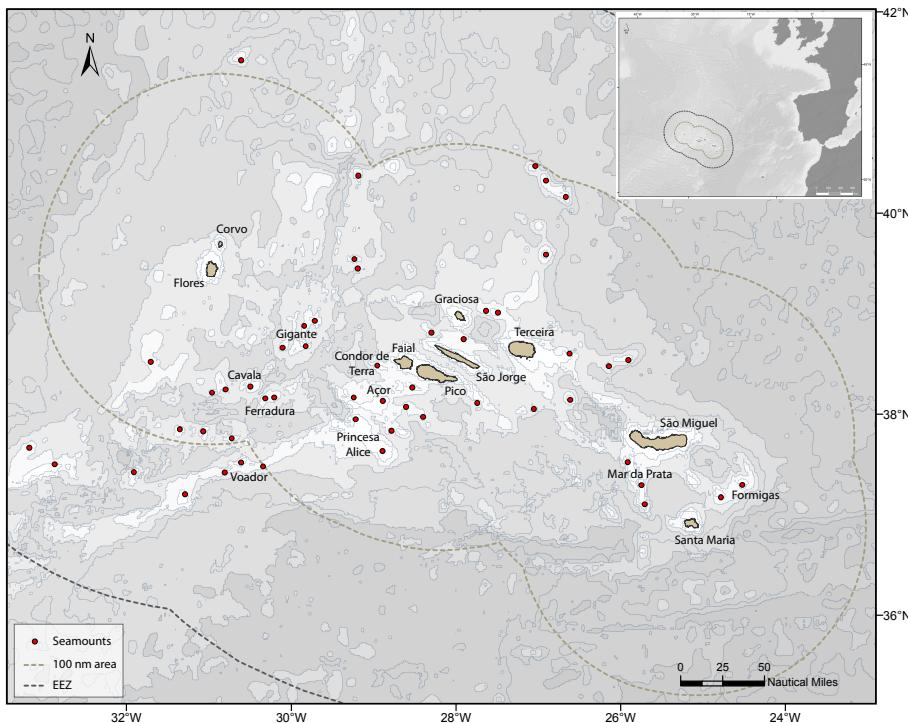


Fig. 1. Map of the study area showing the most important geomorphological features (islands and seamounts) sampled within the Azores EEZ.

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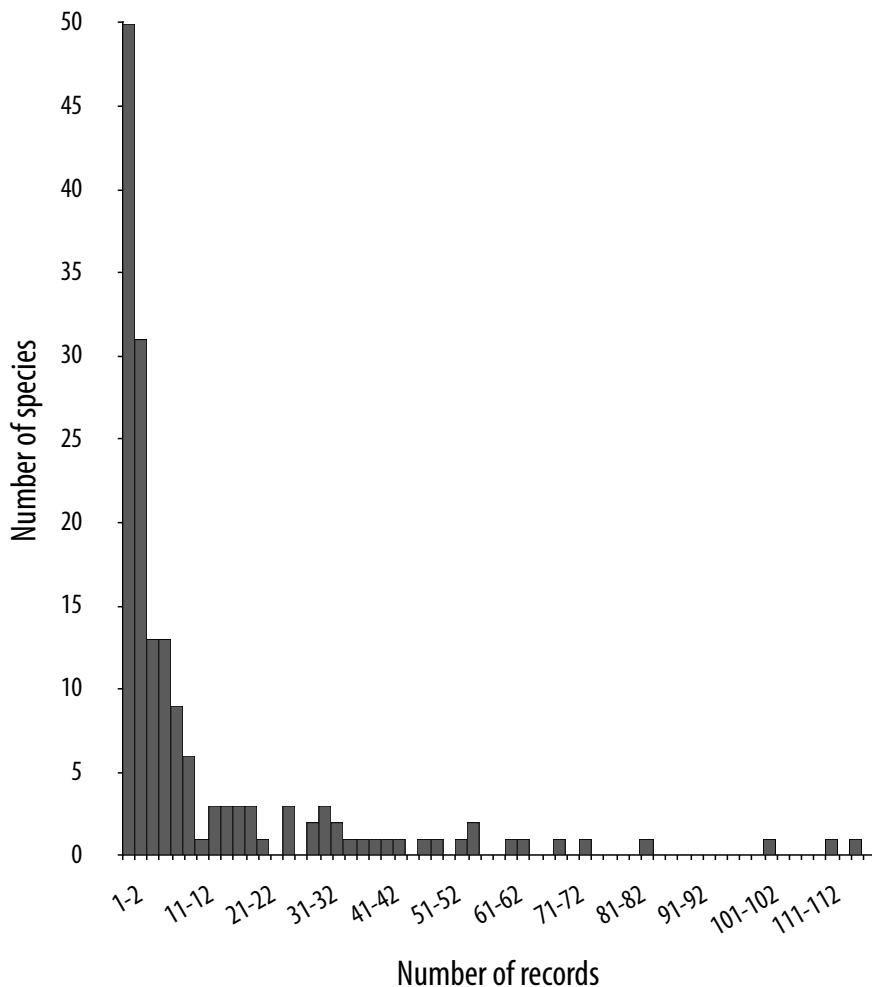


Fig. 2. Distribution of number of species per number of records.

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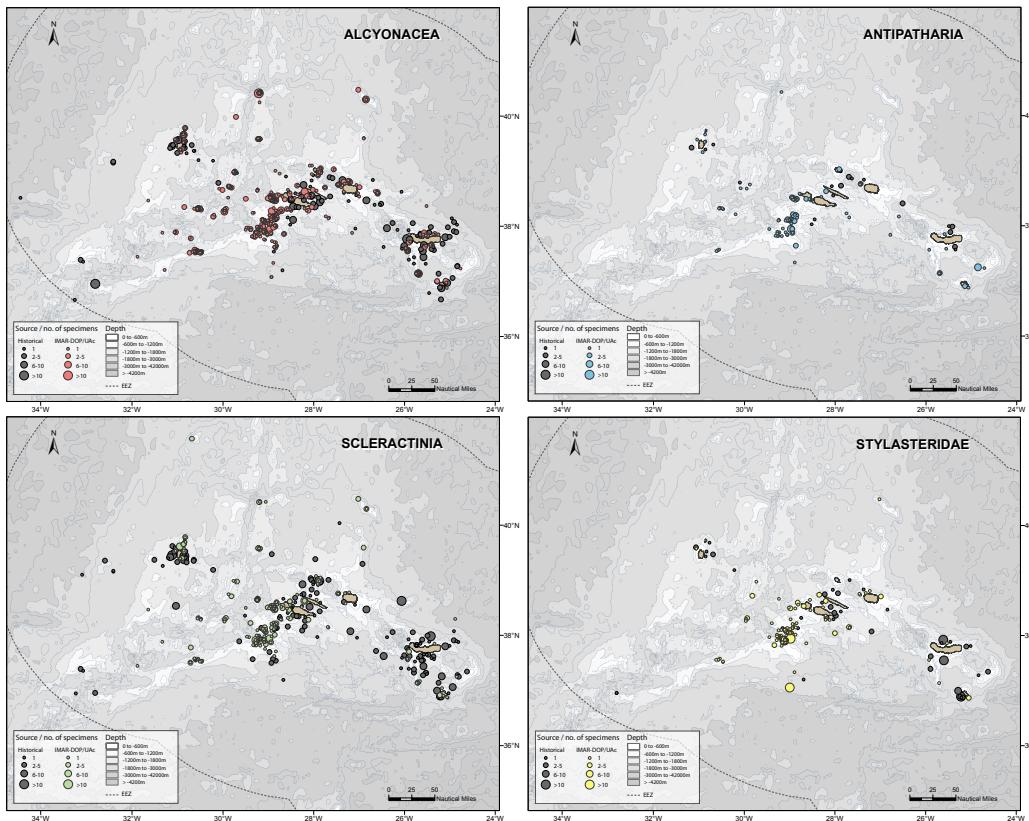


Fig. 3. Distribution of geo-referenced coral records per taxonomic group for the Azores EEZ based on major oceanographic expeditions, other coral events and IMAR-DOP/UAc records, from 1869 to 2011. Alcyonacea: 299 historical/829 IMAR-DOP/UAc records; Antipatharia: 31/120; Scleractinia: 417/327; Stylasteridae: 60/125.

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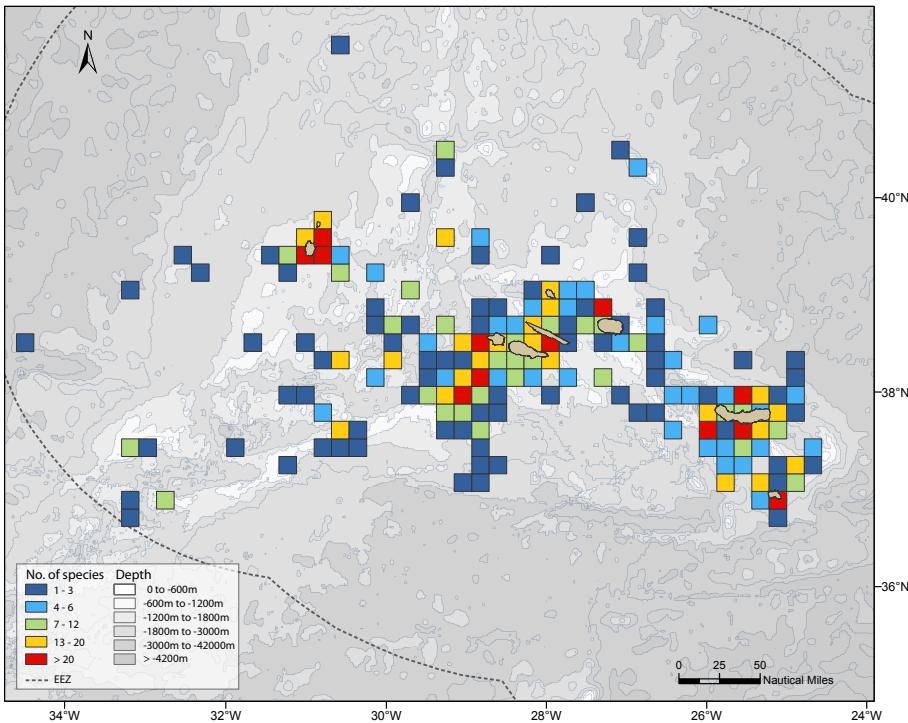


Fig. 4. Species diversity of corals in the Azores EEZ, depicted as total number of species per 20×20 km cells. Samples included 164 species belonging to Alcyonacea, Antipatharia, Scleractinia and Stylasteridae.

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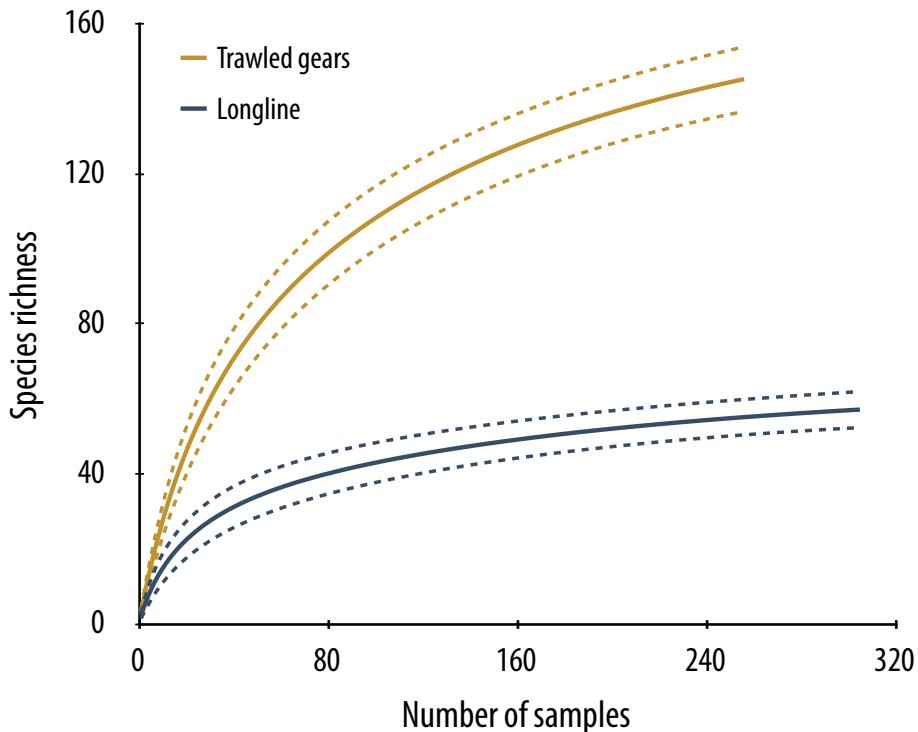


Fig. 5. Sampled-based rarefaction curves for coral fauna by trawled and longline gears. Expected species richness values were calculated using the Mao Tau moment-based estimator with 95 % confidence intervals (dashed lines).

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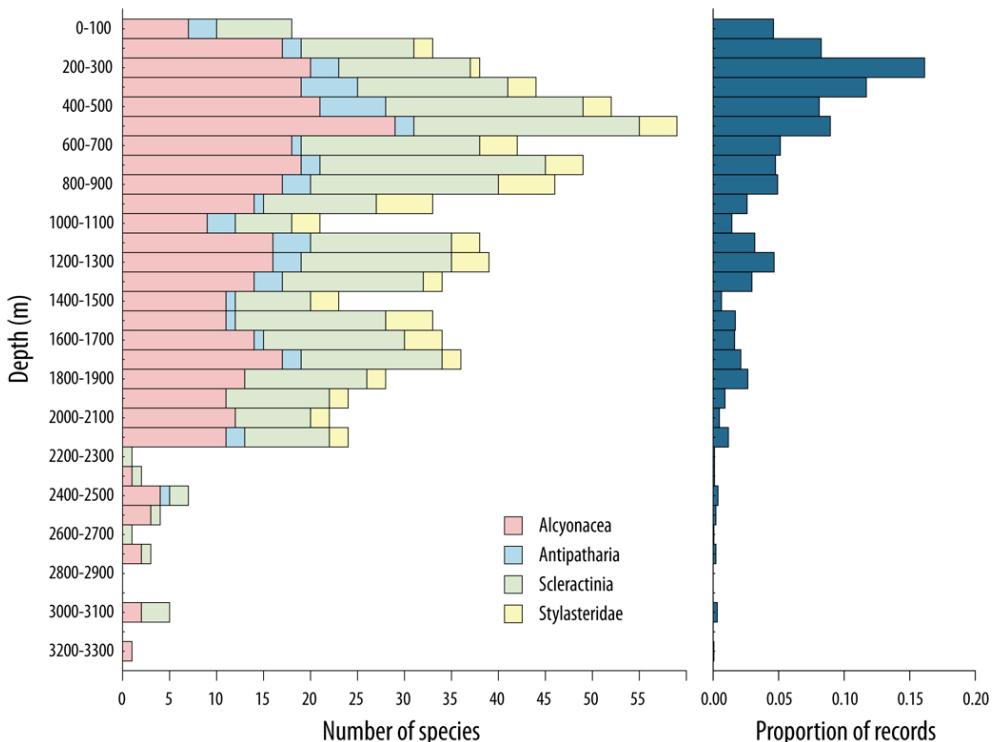


Fig. 6. Summary of depth ranges for Alcyonacea, Antipatharia, Scleractinia and Styelasteridae.

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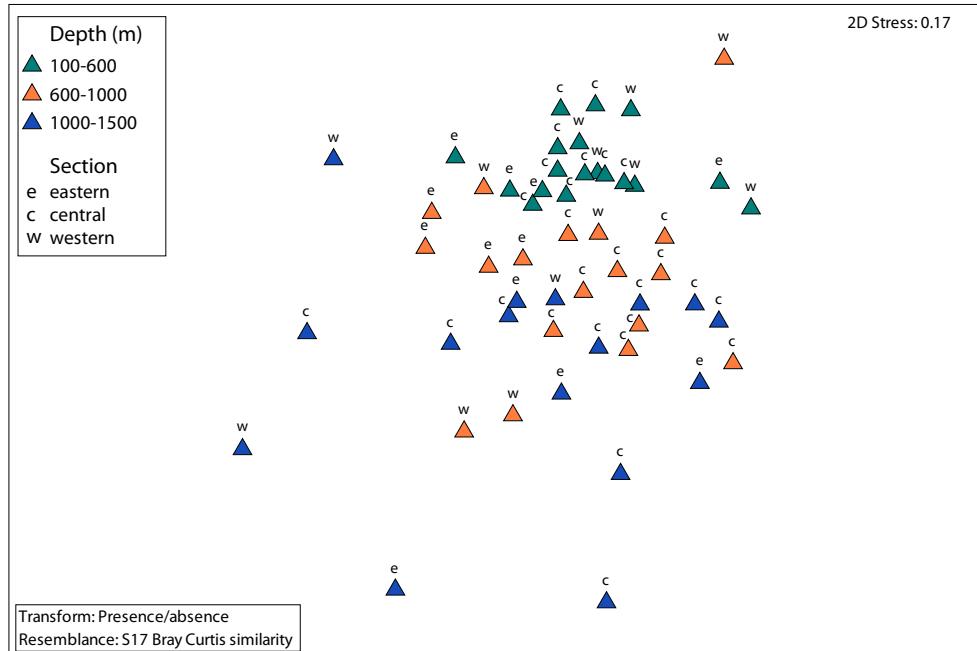


Fig. 7. Non-metric multi-dimensional scaling ordination based on Bray–Curtis similarity coefficients for presence/absence data for features sub-divided by depth intervals.

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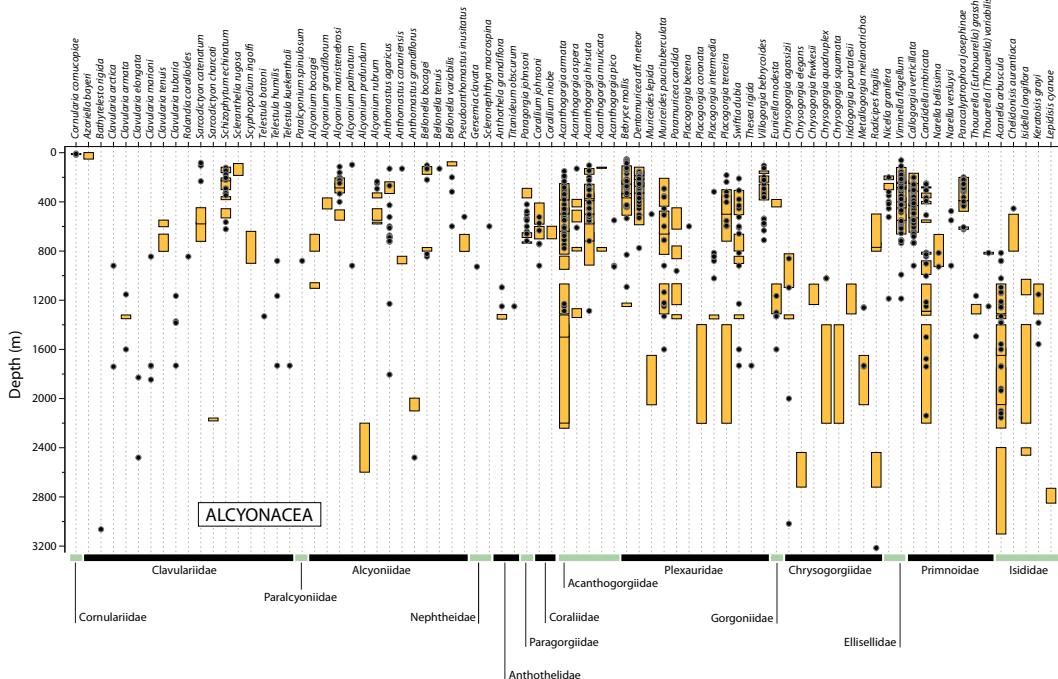


Fig. A1. Species bathymetric ranges. The stylasterid *Stenohelia* sp.A is not represented given that there is no bathymetric information for this record.

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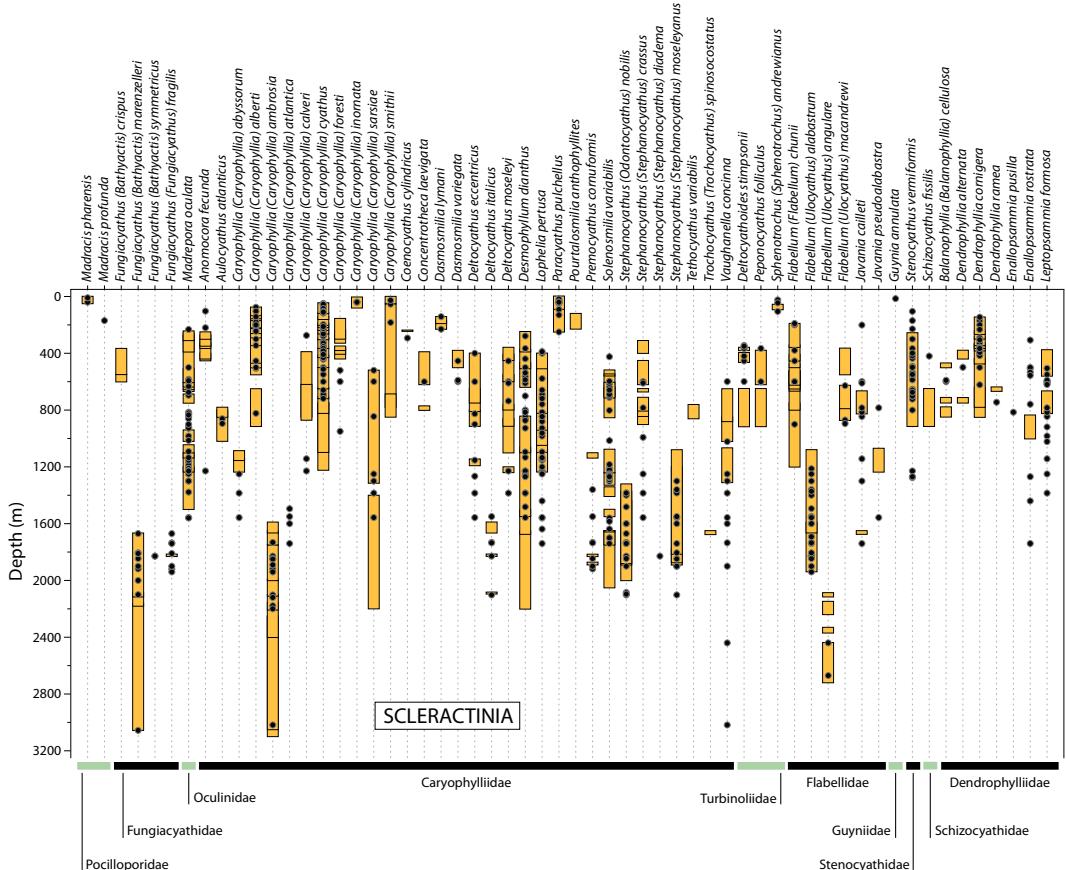


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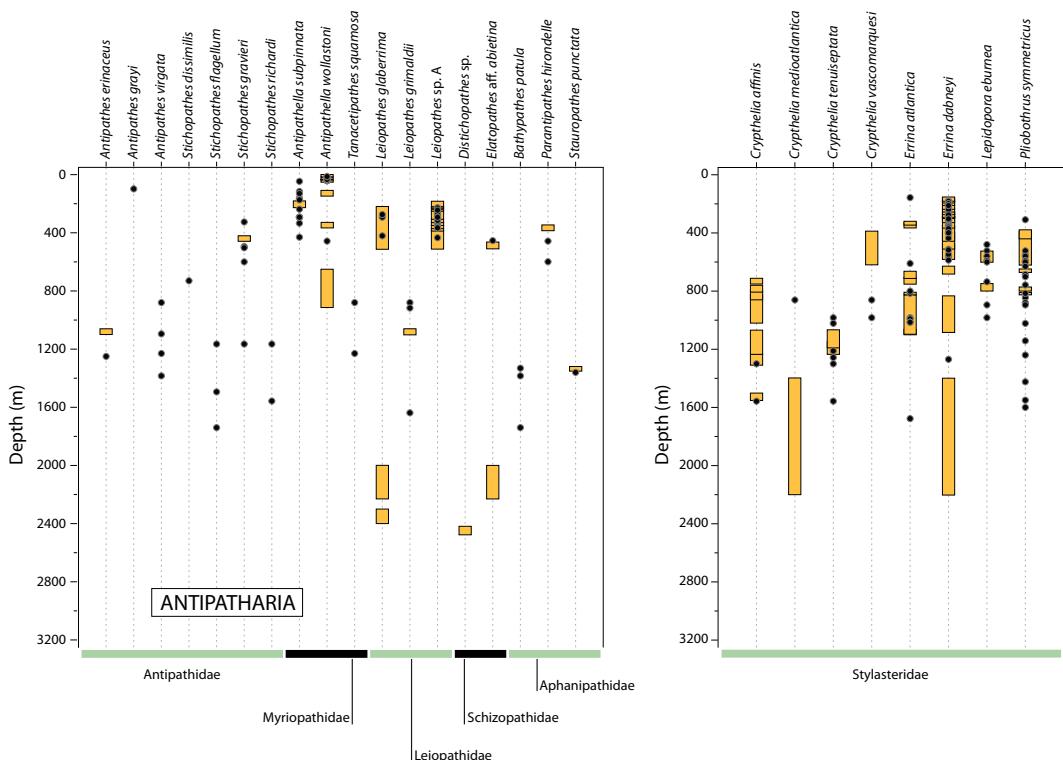


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