



Diversity, distribution and population size structure of deep Mediterranean gorgonian assemblages (Menorca Channel, Western Mediterranean Sea)



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ABSTRACT

Gorgonians are a key group of organisms in benthic marine communities with a wide bathymetric and geographical distribution. Although their presence on continental shelves and slopes has been known for more than 100 years, knowledge concerning the ecology of deep gorgonian species is still in a very preliminary stage. To overcome this situation, gorgonian assemblages located at 40–360 m depth were studied over a large geographical area on the continental shelf and upper slope of the Menorca Channel (Western Mediterranean Sea). A quantitative analysis of video transects recorded by a manned submersible and a remotely operated vehicle, were used to examine the diversity, distribution and demography of gorgonian species. Results showed high gorgonian diversity within this depth range (a total of nine species were observed) compared to Mediterranean coastal areas. Gorgonian assemblages on the continental shelf and upper slope were mostly monospecific (respectively 73% and 76% of occupied sampling units contained one single species), whereas shelf edge assemblages were highly multi-specific (92% of occupied sampling units contained several species). This contrasts with the monospecificity of Mediterranean coastal gorgonian assemblages. Gorgonian populations on the continental shelf were mostly dominated by small colonies (88% of measured colonies) with few intermediate and large colonies (12% of measured colonies). In deeper areas small colonies were still dominant (60% of measured colonies), but intermediate and large colonies were much more abundant (40% of measured colonies). This suggests high recruitment rates on the continental shelf, but perturbations (trammel nets, long lines and strong storms) may limit the presence of intermediate and large colonies. Conversely, on the shelf edge and upper slope a more stable environment may allow colonies to reach larger dimensions. The identification and ecological characterization of these deep assemblages further extends the current knowledge about Mediterranean gorgonians, and is fundamental in improving the management and conservation of deep benthic ecosystems.

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1. Introduction

Gorgonian assemblages play an important structural and functional role in several marine benthic ecosystems all over the world, promoting a high diversity and biomass of associated fauna (Gili and Coma, 1998). From a structural point of view, gorgonians act

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as ecosystem engineers (*sensu* Jones et al., 1994) and foundation species (*sensu* Dayton, 1972) forming complex three-dimensional structures that provide a suitable habitat and refuge for numerous species (Buhl-Mortensen and Mortensen, 2005; Roberts et al., 2009; De Clippele et al., 2015). Current flow, food availability, and sediment re-suspension, vary widely within the complex structures formed by the gorgonian colonies, and this heterogeneity increases the abundance and functional diversity of the associated fauna (Witherell and Coon, 2001; Stone, 2006; Cerrano et al.,

2010). From a functional point of view, gorgonians promote a significant flow of matter and energy from the pelagic to the benthic system by capturing plankton and suspended particulate organic matter (Lewis, 1982; Ribes et al., 1999; Sherwood et al., 2008), playing a paramount role in benthic–pelagic coupling processes and biogeochemical cycles (Gili and Coma, 1998; Coma et al., 2001; Hill et al., 2014).

Knowledge about diversity, distribution, ecology and state of conservation of gorgonian assemblages in coastal areas has significantly increased in recent decades based on the research carried out within the depth range of traditional scuba diving (~40 m depth) (e.g. Grigg, 1977; Yoshioka and Yoshioka, 1989; Linares et al., 2008). Far less is known about deep gorgonian assemblages located on the continental shelf and slope (e.g. Mortensen and Buhl-Mortensen, 2004; Matsumoto et al., 2007; Salomidi et al., 2009; Stone et al., 2014), where gorgonian presence was mostly known due to specimens by-cached by fishermen or withdrawn by blind destructive techniques (Relini et al., 1986) for taxonomical studies (Carpine and Grasshoff, 1975; Grasshoff, 1992). The most recent technological development and increased availability of remotely operated vehicles (ROVs), manned submersibles, and video-equipped towed gears have significantly increased accessibility to deeper areas, allowing for controlled sampling and quantitative study of deep rocky bottoms communities (e.g. Reed et al., 2006; Mortensen et al., 2008; Orejas et al., 2009). Abiotic features change considerably with depth (Bell and Barnes, 2000; Garrabou et al., 2002; Bak et al., 2005), and the overall variability in environmental conditions is dampened at greater depths (below ~100 m depth) because temperature, currents, and other water column features are more constant than in shallower areas (e.g. Puig et al., 2000; De Mole et al., 2002; Fernández de Puelles et al., 2007). Such stability in the main environmental conditions could allow deep gorgonians to grow larger and develop populations dominated by medium and large-sized colonies (Grigg, 1975; Watanabe et al., 2009; Gori et al., 2011b). Toppling and detachment by strong currents or wave action is considered one of the main causes of mortality of large gorgonian colonies (Grigg, 1977; Weinbauer and Velimirov, 1996; Weinberg and Weinberg, 1979). Indeed, both the environmental suitability and stability of a habitat may be reflected in the size structure of gorgonian and coral populations, because the size structure reflects the factors affecting recruitment, growth, and mortality rates in a particular habitat for a period of time matching the longevity of the population (Grigg, 1975; Gilmour, 2004; Alvarado-Chacón and Acosta, 2009).

Earlier ecological studies on deep gorgonian assemblages in the Mediterranean Sea revealed that they can reach density values as high as those observed in littoral environments (e.g. Bo et al., 2009; Angiolillo et al., 2014). However, both the continental shelf and upper slope are areas where fishing is more intense (Watling and Norse, 1998; Hall-Spencer et al., 2002). Gorgonians are among the most common species of the by-catch of bottom trawling, trammel nets, and long line fishing (Van Dolah et al., 1987; Krieger, 2001; Mytilineou et al., 2014). Since gorgonians are usually long-lived and slow growing (Linares et al., 2007; Risk et al., 2002; Sherwood and Edinger, 2009), fishing impacts can have far-reaching and long-lasting effects (Althaus et al., 2009). Consequently, deep gorgonian assemblages located on the continental shelf and upper slope are nowadays highly threatened by fishing activity (Hall-Spencer et al., 2002), and knowledge about their diversity, distribution and state of conservation is urgently needed to implement effective management and conservation measures of deep benthic ecosystems.

To this purpose, the aims of this study were: (1) to characterize the diversity and quantify the abundance of gorgonians forming Mediterranean gorgonian assemblages on a large area of the conti-

mental shelf and upper slope at 40–360 m depth (2) to assess the geographical and vertical distribution patterns of the observed species; (3) to appraise their population size structure, and (4) to gain insight into the possible factors affecting their abundance and distribution.

2. Material and methods

2.1. Study area

The Menorca Channel is located in the Western Mediterranean Sea between Mallorca and Menorca Islands (39°53'0.73"N, 3°29'51.16"E) (Fig. 1a), as part of the Balearic Promontory (Acosta et al., 2002). The continental shelf in this area extends between 40 and ~110 m depth, and is largely covered by maërl alternating with patches of coastal detritic sediments and coralligenous outcrops (Barberá et al., 2012). Conversely, smooth reliefs and large extensions of detritic sediments with few isolated patches of outcropping rocks characterize most of the shelf edge and continental slope. Only near Cap Formentor (Fig. 1b) and in the Menorca Canyon (Fig. 1c) sharply edged rock outcroppings and rocky vertical walls are the dominant substrates.

The northern shelf edge and continental slope of the study area is mainly influenced by the Balearic Current (Balbín et al., 2012) and its associated front (Ruiz et al., 2009), which originates from a branch of the Liguro-Provençal-Catalan current, flowing northward over the continental slope of the Balearic archipelago at ~200 m depth (López García et al., 1994; Ruiz et al., 2009). Secondary currents flow northward from the Algerian subbasin entering the Balearic subbasin and feed the Balearic current (Alemany et al., 2006; Amores et al., 2013). Conversely, the southern shelf edge and upper slope is not influenced by a steady current (Amores and Monserrat, 2014), but by the sporadic arrival of mesoscale structures detached from the Algerian Current and the Almería-Oran front (Millot, 1987; García et al., 2005).

2.2. Sampling procedure

A total of 73 video transects (Fig. 1a, Supplementary material 1) were recorded during five surveys conducted on board of the R/V “García del Cid” (September 2010, April 2011, October 2011, June 2012) and the R/V “Miguel Oliver” (August 2011). During the first two surveys, 20 video transects were recorded with the manned submersible JAGO (IFM-GEOMAR), whereas 53 video transects were recorded with the ROV NEMO (Gavin Newman) during the last three campaigns. Both instruments were equipped with a 1080 horizontal line resolution camera, a grabber and two parallel laser beams which provided a scale to define a fixed width of the transects (0.3 m) during the subsequent video analysis. Transects were recorded in a close-zoom (~0.5 to 1.5 m width of view) and in a digital format. Positioning of JAGO and NEMO was achieved with underwater acoustic positioning system (LinkQuest TrackLink 1500 HA). Both JAGO and NEMO moved at a constant speed of ~0.3 knots, and transect lengths ranged between 309 and 2375 m, over depths ranging from 52 to 347 m. Transects were haphazardly located in order to cover the whole study area, but areas showing morphological features possibly related to the presence of rocky bottoms were explored more intensively (Fig. 1 and Supplementary material 1). Overall, a total of 57.8 km was video recorded along the seabed.

In order to confirm the taxonomic identification of the species observed in the video-transects, voucher colonies of gorgonian species observed along the transects were also collected (Supplementary material 2). Colonies were fixed and preserved in 10% formalin until analyzed in the laboratory.

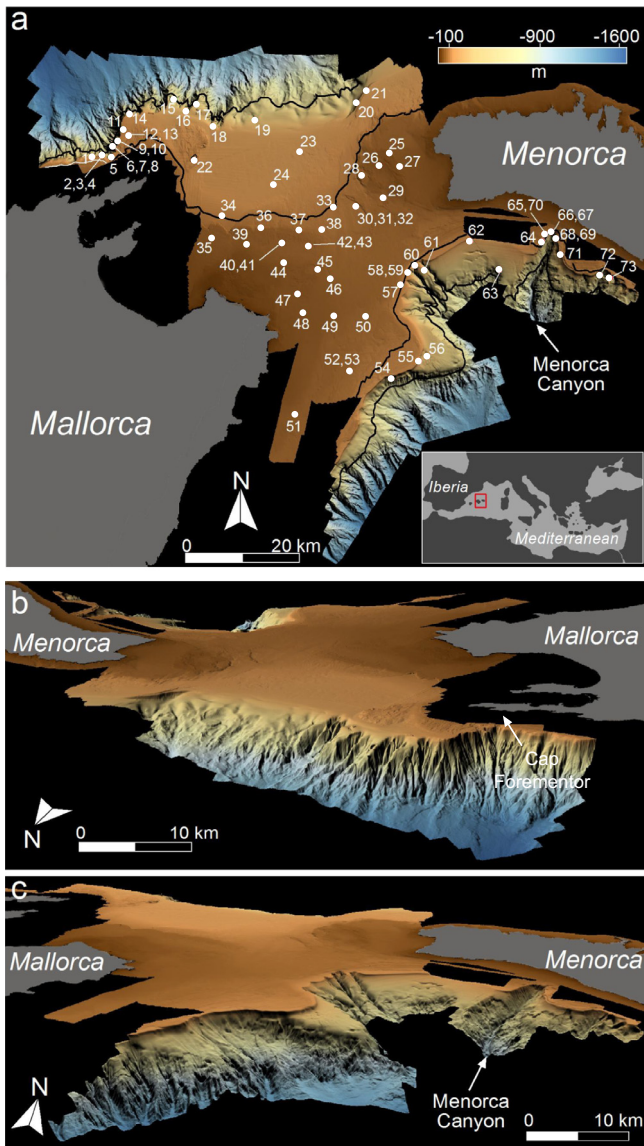


Fig. 1. The study area. (a) Three-dimensional bathymetry of the Menorca Channel: the map shows the location of the video transects (1–73) and the location of the study area in the western Mediterranean. Detail of the (b) northern and (c) southern subareas.

2.3. Video analysis

Quantitative video analysis was performed according to the methodology described in Gori et al. (2011a) using Apple's Final Cut Pro software. All the pauses in the movement of the JAGO or NEMO were removed from the footage, in order to correctly estimate the length in each transect, and those sequences with poor image quality or too far away from the seafloor were considered unsuitable for analysis. The remaining useful sequences comprised 94.6% of the total recorded material and corresponded to a total distance of 54.7 km. Every gorgonian observed within a width of 0.3 m (based on the laser beams) along each video transect was identified with a time reference derived from the time elapsed since the beginning of the video transect to the crossing of the laser beams with the base of the colony (Gori et al., 2011a). This time reference was posteriorly converted into position along the transect according to known velocity ($P = t \cdot v$, where t is the time reference expressed in seconds, and v is the velocity expressed in

meters per second). A similar procedure was used to characterize seabed substrate types and slope along every transect, within the same width of 0.3 m. Seabed substrate type was classified (based on the Wentworth scale) into four categories: sand to gravel, cobbles and pebbles, maërl, and rock. Seabed slope was classified into three categories: horizontal (0–30°), sloping (30–80°) and vertical (80–90°); slope was estimated from the video by looking at the two parallel laser beams and the depth sensor (Gori et al., 2011a; Ambroso et al., 2013).

To study population size structure, the maximum height of each observed gorgonian colony was measured using the Macnification 2.0.1 software (Schols and Lorson, 2008) on still images extracted from recorded footage. The distance from the two lasers beams was used to calibrate the images. Measurements were done on still images in which the colony base was in the same plane as the laser beams, while the colony lied perpendicular to the video (Gori et al., 2011b). This methodological constraint entails that only a subsample of observed gorgonians could be measured for the study of population size structure (81% of the total observed colonies, 63–100% of the colonies in each transect).

2.4. Species identification

Identification of the observed species was based on the existing taxonomic works on Atlanto-Mediterranean gorgonians (Carpine and Grasshoff, 1975; Grasshoff, 1992), and confirmed by the examination of the voucher specimen collected (see Section 2.2), looking at the colonial branching pattern, the distribution and shape of calyces and polyps along branches, as well as the shape and size of sclerites. For this purpose, small fractions of the sampled colonies were placed in a sodium hypochlorite solution until organic matter was dissolved and sclerites disaggregated. Sclerites were rinsed with distilled water, and observed under a stereoscope (Olympus SZ-60). Three *Paramuricea macropsina* (Koch, 1882) morphotypes were differentiated in the video, two chromatic morphotypes on the continental shelf (M1, M2) and a third one on the shelf edge (M3) (more details in Grinyó et al., submitted for publication) (Fig. 2c, d and e).

2.5. Data treatment

2.5.1. Gorgonian occupancy and abundance

To quantify gorgonian occupancy (frequency of occurrence in the set of sampling units) and abundance (number of colonies per sampling unit), and examine the species composition of gorgonian assemblages within the study area, each transect track was divided into a string of 2 m² (0.3 m width and 6.66 m long) sampling units, using ArcMap 10.1 software (ESRI ArcGIS ArcInfo v10). Such sampling unit size was chosen as representative of Mediterranean octocorals on rocky substrate (based on Weinberg, 1978), as well as to allow a comparison with previous studies on shallow gorgonian and coral species (Gori et al., 2011a; Ambroso et al., 2013). A total of 8221 sampling units were obtained from the 73 transects, corresponding to a total area of 0.016 km². Each sampling unit was characterized by the number of colonies of each gorgonian species, as well as by its depth and coverage percentage for each substrate and slope type. For each gorgonian species, occupancy and abundance were quantified. Gorgonian assemblages were assessed based on species composition using a non-metric multidimensional scaling ordination (nMDS) of the sampling units, with gorgonian abundances square root transformed, and ordination by a Bray–Curtis similarity matrix. Adonis permutation multivariate analysis of variance and subsequent pairwise tests were used to test for significance of differences in gorgonian assemblages based on depth: continental shelf (40–100 m depth), shelf edge (100–180 m depth), upper slope

(180–360 m depth), as well as substrate type (sand to gravel, cobbles and pebbles, maërl and rock), and slope (horizontal, sloping and vertical). Dominant substrate and slope type was assigned to each sampling unit for this analysis. Ordination and permutation multivariate analysis of variance and subsequent pairwise tests were performed using the R-language functions *metaMDS* and *adonis*, respectively, which are available in the *vegan* library of the R software platform (R Core Team 2014). The *adonis* test was performed considering depth, substrate and slope simultaneously. Additionally, a similarity percentage procedure analysis (SIMPER, Clarke and Warwick, 1994) was performed to identify which gorgonian species contributed the most to the different assemblages considering the previously mentioned environmental features using the software PRIMER v6 (Clarke and Warwick, 2001).

2.5.2. Geographical and vertical distribution

Geographical distribution of each species in the study area was studied by mapping the observed density on a geographically ref-

erenced map using GIS (ESRI ArcGIS ArcInfo v10). Vertical distribution of each species was studied grouping sampling units in 20 m depth intervals (based on their depth), and estimating the median (first and third quartile, and the range between minimum and maximum values) of gorgonian density in each depth interval.

2.5.3. Population size structure

Size structure of gorgonian populations was analyzed in terms of descriptive statistics using distribution parameters such as skewness and kurtosis. Skewness is a measure of the symmetry of a distribution using its mean, reflecting the proportion of small versus large colonies in a gorgonian population. If skewness is significant ($p < 0.05$) population size structure is asymmetrical. Positive skewness denotes the prevalence of small size colonies, while negative skewness denotes the dominance of large size colonies in the population. Kurtosis is a measure of the peakedness of a distribution near its central mode. A significant kurtosis value ($p < 0.05$) indicates longer tails than would be expected for a

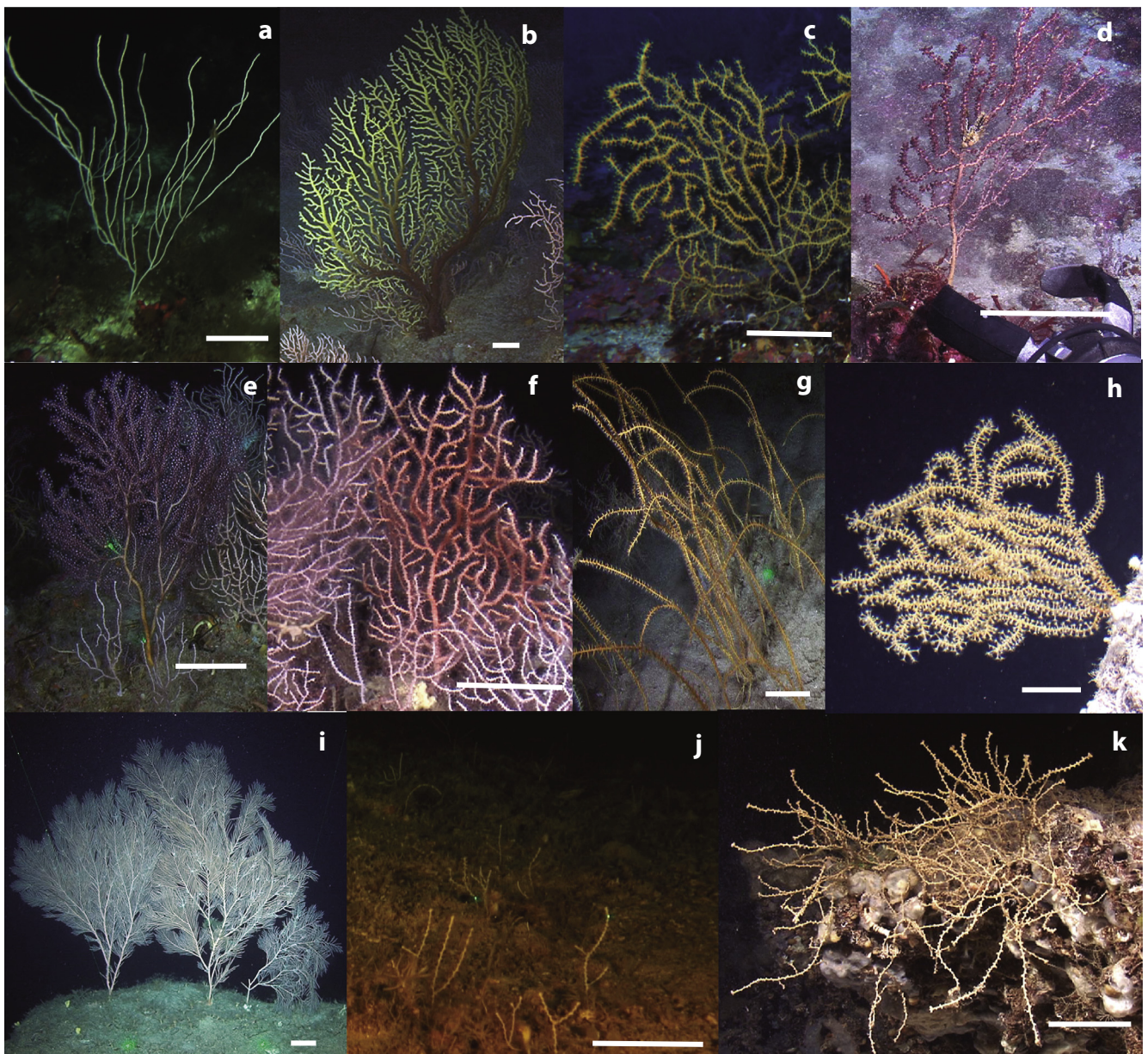


Fig. 2. Studied species images. (a) *Eunicella singularis*, (b) *Paramuricea clavata*, (c) *Paramuricea macrospina* morphotypes (M1), (d) M2, (e) M3, (f) *Eunicella cavolinii*, (g) *Viminella flagellum*, (h) *Acanthogorgia hirsuta*, (i) *Callogorgia verticillata*, (j) *Swiftia pallida*, and (k) *Bebryce mollis*. Scale Bar: 10 cm.

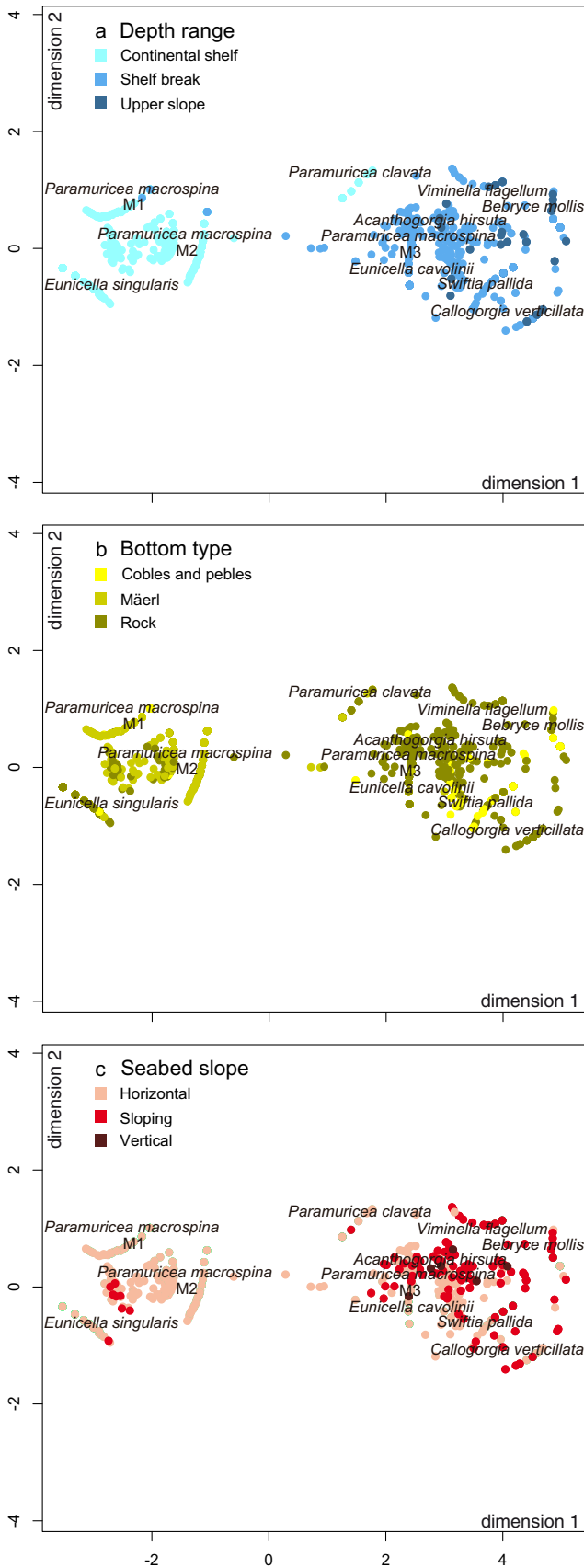


Fig. 3. Non-metric multidimensional scaling (nMDS) ordination plot. Gorgonian abundance was square root transformed and analysis performed on Bray–Curtis dissimilarity matrix. Sampling units ($n = 1562$) containing gorgonians are represented considering (a) depth range, (b) bottom type and (c) seabed slope. A stress estimate of 0.025 was obtained.

located on maërl beds, and *V. flagellum* dominate in vertical rocky bottoms (Table 2).

3.2. Geographic and vertical distribution

Only three species were observed on the continental shelf of the study area, *P. macrospina* (M1, M2), *E. singularis* and *Paramuricea clavata* (Risso, 1826) (Fig. 4, Table 1). *P. macrospina* (M1, M2) and *E. singularis* were the most frequent species scattered over the continental shelf (Fig. 4) at 65–100 m and 52–88 m depth, respectively (Fig. 5). Both morphotypes of *P. macrospina* were much more abundant in terms of colony number than *E. singularis* (Table 1). Conversely, *P. clavata* was only found on the continental shelf in two low-density patches on coralligenous banks at 67–92 m depth, and few colonies on the shelf edge at 109–120 m depth (Figs. 4 and 5). The shelf edge and upper slope were much more diverse than the continental shelf in terms of species richness. In this depth range, gorgonian assemblages were highly localized in the areas dominated by rocky outcrops and vertical walls near Cap Formentor and in the Menorca Canyon (Fig. 4). *E. cavolinii* was the most frequent and abundant species of the shelf edge, with the

Table 2

SIMPER analysis. Species that belong to the similarity group of 90% of cumulative contribution are present. Percentages in bold letters are the average similarity values for each category.

Depth range	Sim/SD	Contribution %	Cum. contribution %
Continental shelf: 22.43%			
<i>E. singularis</i>	0.48	60.33	60.33
<i>P. macrospina</i> M1	0.34	24.59	84.92
<i>P. macrospina</i> M2	0.25	14.86	99.79
Shelf edge: 21.45%			
<i>E. cavolinii</i>	0.65	78.43	78.43
<i>S. pallida</i>	0.25	14.70	93.14
Upper slope: 17.89%			
<i>B. mollis</i>	0.33	38.55	38.55
<i>C. verticillata</i>	0.26	24.83	63.38
<i>S. pallida</i>	0.27	23.30	86.68
<i>V. flagellum</i>	0.21	12.13	98.81
Bottom type			
Rock: 18.63%			
<i>E. singularis</i>	0.37	54.89	54.89
<i>E. cavolinii</i>	0.33	32.61	87.50
<i>S. pallida</i>	0.12	3.68	91.19
Cobbles & pebbles: 17.67%			
<i>S. pallida</i>	0.42	60.77	60.77
<i>E. cavolinii</i>	0.21	14.08	74.85
<i>P. macrospina</i> M1	0.16	10.86	85.70
<i>B. mollis</i>	0.15	9.93	95.64
Maërl: 28.68%			
<i>P. macrospina</i> M1	0.62	60.20	60.20
<i>P. macrospina</i> M2	0.42	33.55	93.75
Seabed slope			
Horizontal: 18.11%			
<i>E. singularis</i>	0.35	49.09	49.09
<i>P. macrospina</i> M1	0.28	25.11	74.19
<i>P. macrospina</i> M2	0.29	14.93	89.13
<i>E. cavolinii</i>	0.15	7.12	96.25
Sloping: 19.66%			
<i>E. cavolinii</i>	0.50	66.28	66.28
<i>B. mollis</i>	0.17	9.94	76.22
<i>S. pallida</i>	0.17	9.26	85.48
<i>V. flagellum</i>	0.17	7.03	92.51
Vertical: 31.68%			
<i>E. cavolinii</i>	0.56	53.09	53.09
<i>V. flagellum</i>	0.51	44.75	97.84

highest abundances concentrated at 100–160 m depth, together with *P. macrospina* M3 (Figs. 4 and 5). *V. flagellum*, *S. pallida*, *C. verticillata* were also abundant on the shelf edge, but extended their distribution beyond 240 m depth, with one colony of *S. pallida* observed at 324 m (Figs. 4 and 5). *Acanthogorgia hirsuta* Gray, 1857 was the species showing the most restricted distribution, occurring in few locations of the shelf edge at 149–176 m depth (Fig. 5). *B. mollis* extended its distribution from the shelf edge to the upper slope, where it was the most frequent species, followed by *C. verticillata* and *V. flagellum* (Table 1). *V. flagellum* was the most abundant species in the upper slope, followed by *S. pallida*, *B. mollis* and *C. verticillata* (Table 1). Finally, some colonies (~20) of the precious coral, *Corallium rubrum*, were observed at 80–120 m depth, whereas only few isolated colonies were seen below 150 m depth.

3.3. Population size structure

Overall, the maximum height of 81% of all the observed colonies was measured (63–100% of the colonies in each transect). All the analyzed populations, indistinctively of the species, were unimodal (Figs. 6a and 6b). Most populations of *P. macrospina* M1, *V. flagellum* and the only analyzed population of *C. verticillata* were positively skewed, indicating the dominance of small colonies (Figs. 6a and 6b and Table 3). Conversely, most population of *P. macrospina* M2, *E. cavolinii*, *S. pallida* and all the *E. singularis* populations were not skewed, being dominated by medium sized colonies (Figs. 6a and 6b and Table 3). One of the two-studied populations of *P. macrospina* M3 was positively skewed (Fig. 6b and Table 3). All

the *P. macrospina* M1 populations showed significant kurtosis (Table 3), indicating that they were slightly more peaked or over-centralized than normal distributions; conversely, only a few populations showed significant kurtosis in the other species (Table 3). The shrub like morphology, and the densely intertwined branches of *B. mollis* did not allow the study of population size structure in this species.

3.4. Relationship with environmental features

Depth, substrate and slope explained ~20.8% of the total inertia (i.e. explained variation of the data) in the CCA, with the first two axis accumulating 17.1% of the species variances, and 82.3% of the species-environment relation variance (Fig. 7). According to the Monte Carlo permutation test, the three factors contributed significantly ($p < 0.001$) to the ordination. Depth clearly segregates gorgonians found on the continental shelf (*P. macrospina* M1 and M2, *E. singularis*, *P. clavata*) from those from the shelf edge and continental slope (*P. macrospina* M3, *V. flagellum*, *E. cavolinii*, *S. pallida*, *B. mollis*, *C. verticillata*, and *A. hirsuta*). On the continental shelf, *P. macrospina* M1 and M2 were mainly associated with horizontal maërl beds, whereas *E. singularis* and *P. clavata* with rocky bottoms (Fig. 7). On the shelf edge and continental slope, *E. cavolinii* and *P. macrospina* M3 were mainly associated with sloping rocky bottoms. At increasing depth *V. flagellum*, *S. pallida*, *C. verticillata*, and *A. hirsuta* were also mainly associated with sloping bottoms (Fig. 7). Finally, *B. mollis* was the species most strongly associated with highest depths (Fig. 7).

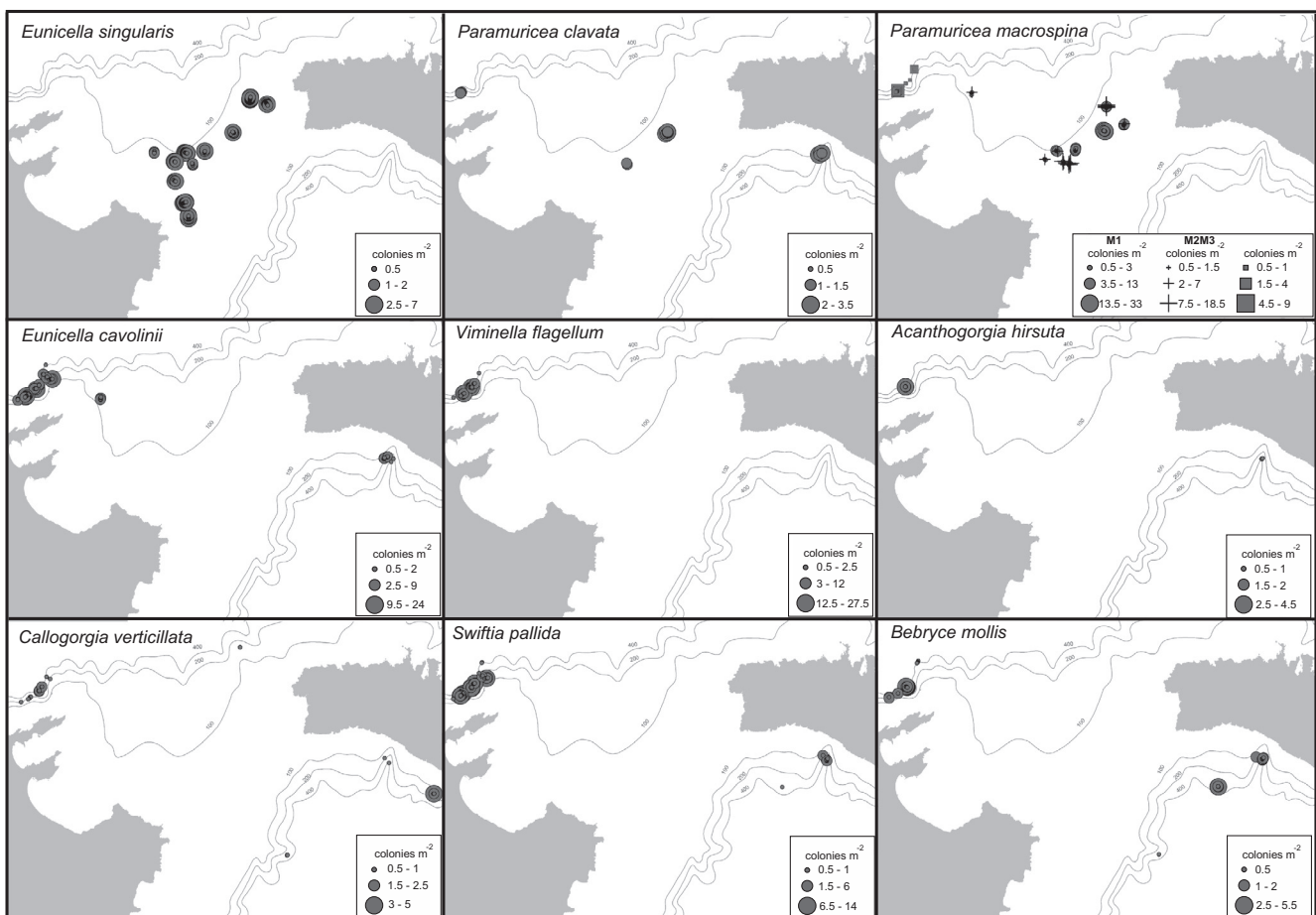


Fig. 4. Geographical distribution. *E. singularis*, *P. clavata*, *P. macrospina* (M1, M2, M3), *E. cavolinii*, *V. flagellum*, *A. hirsuta*, *C. verticillata*, *S. pallida* and *B. mollis* distribution is represented on the study area based on sampling unit density. Species have been displayed from shallowest to deepest distribution.

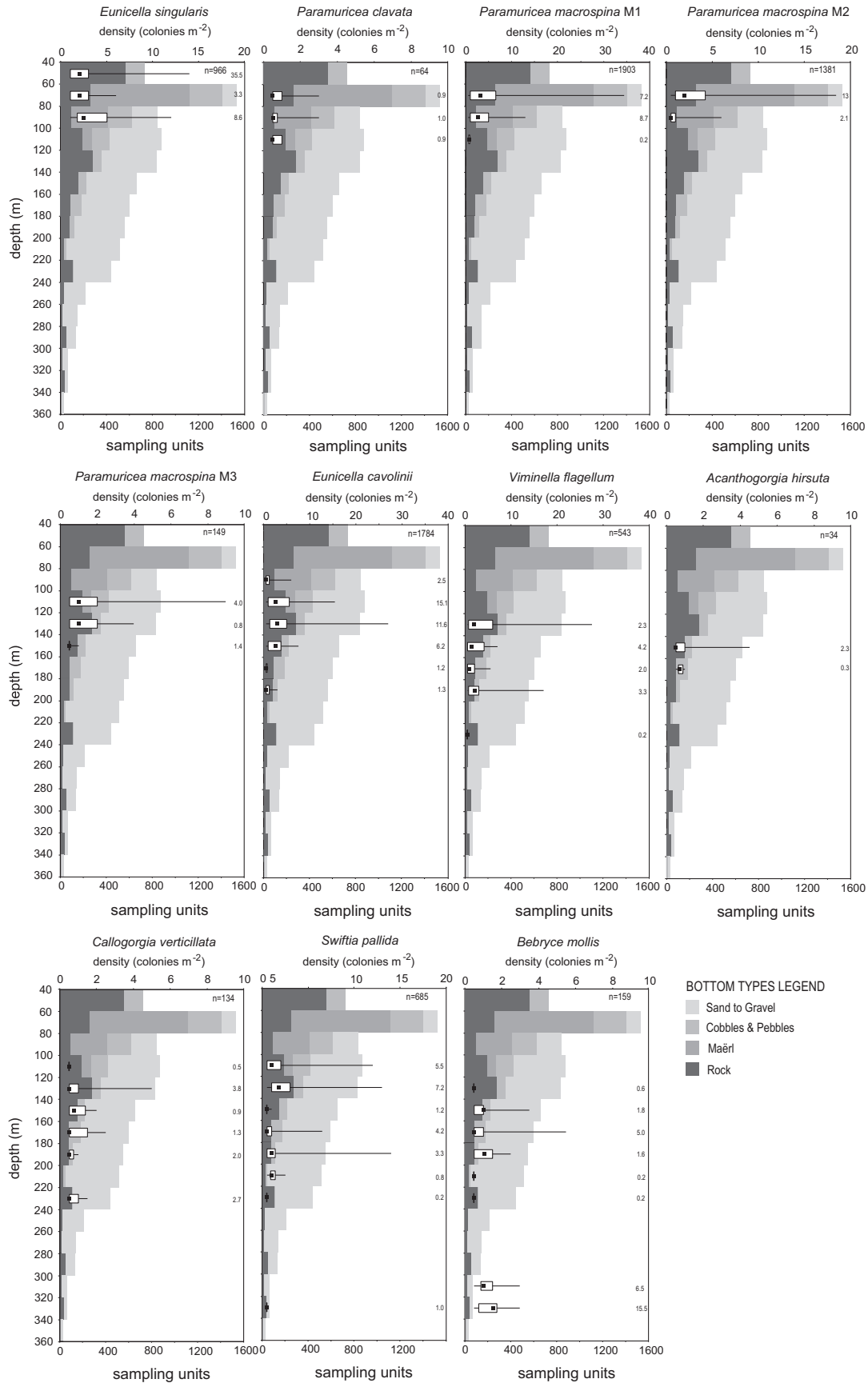


Fig. 5. Vertical distribution. *E. singularis*, *P. clavata*, *P. macrospina* (M1, M2, M3), *E. cavolinii*, *V. flagellum*, *A. hirsuta*, *C. verticillata*, *S. pallida* and *B. mollis* distribution is represented along the studied bathymetric range based on sampling unit density. Black square indicates the median value; the box indicates the first and third quartiles; and the line indicates the range between minimum and maximum values. Gray-scale histograms represent the total number of sampling units for each substrate type (see legend) over the studied bathymetric range. The numbers on the right indicate the percentage of sampling units with species presence (n = number of colonies).

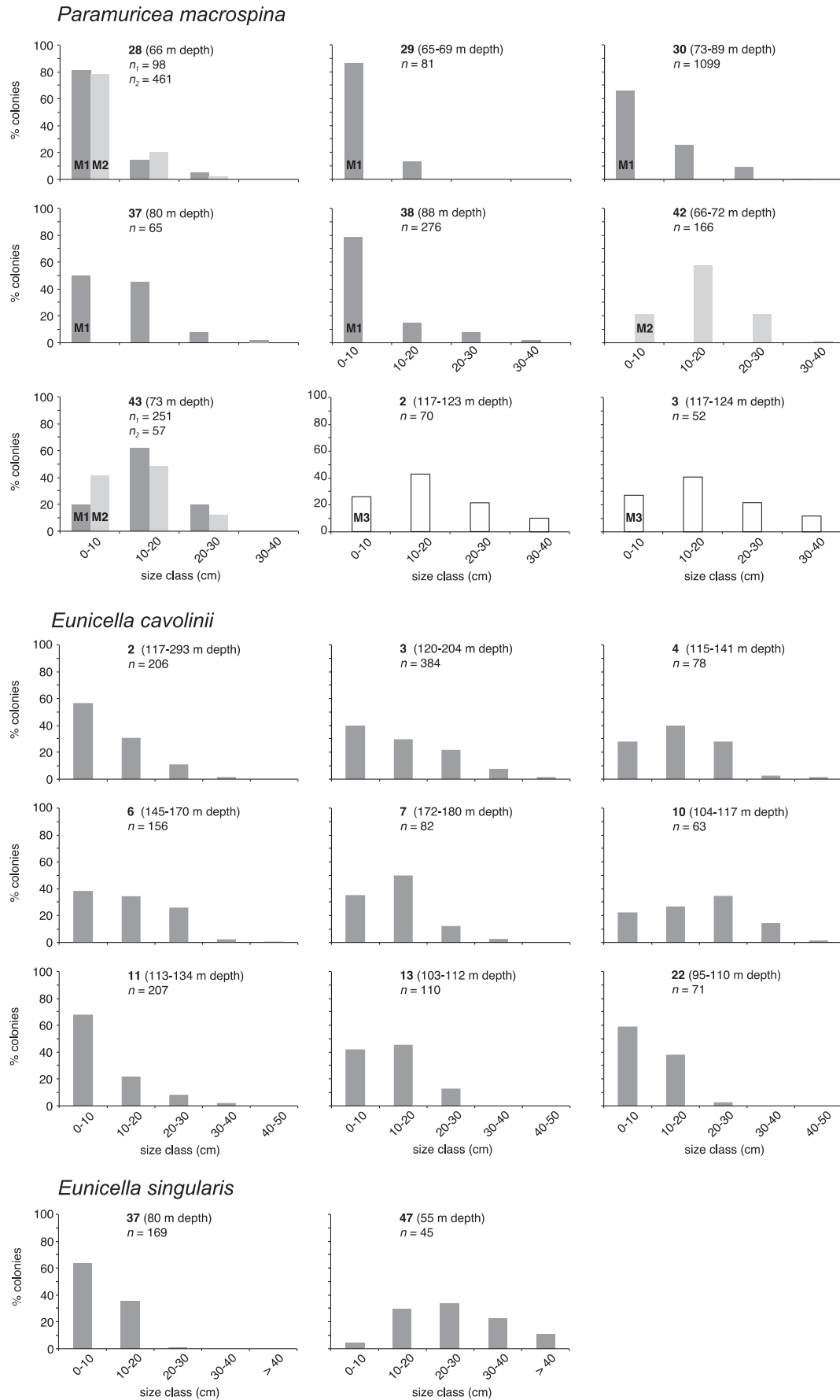


Fig. 6a. *P. macrospina* (M1, M2, M3), *E. cavolinii* and *E. singularis* population size frequency distribution (transect number as in Fig. 1 and Table 3, depth range, n = number of colonies).

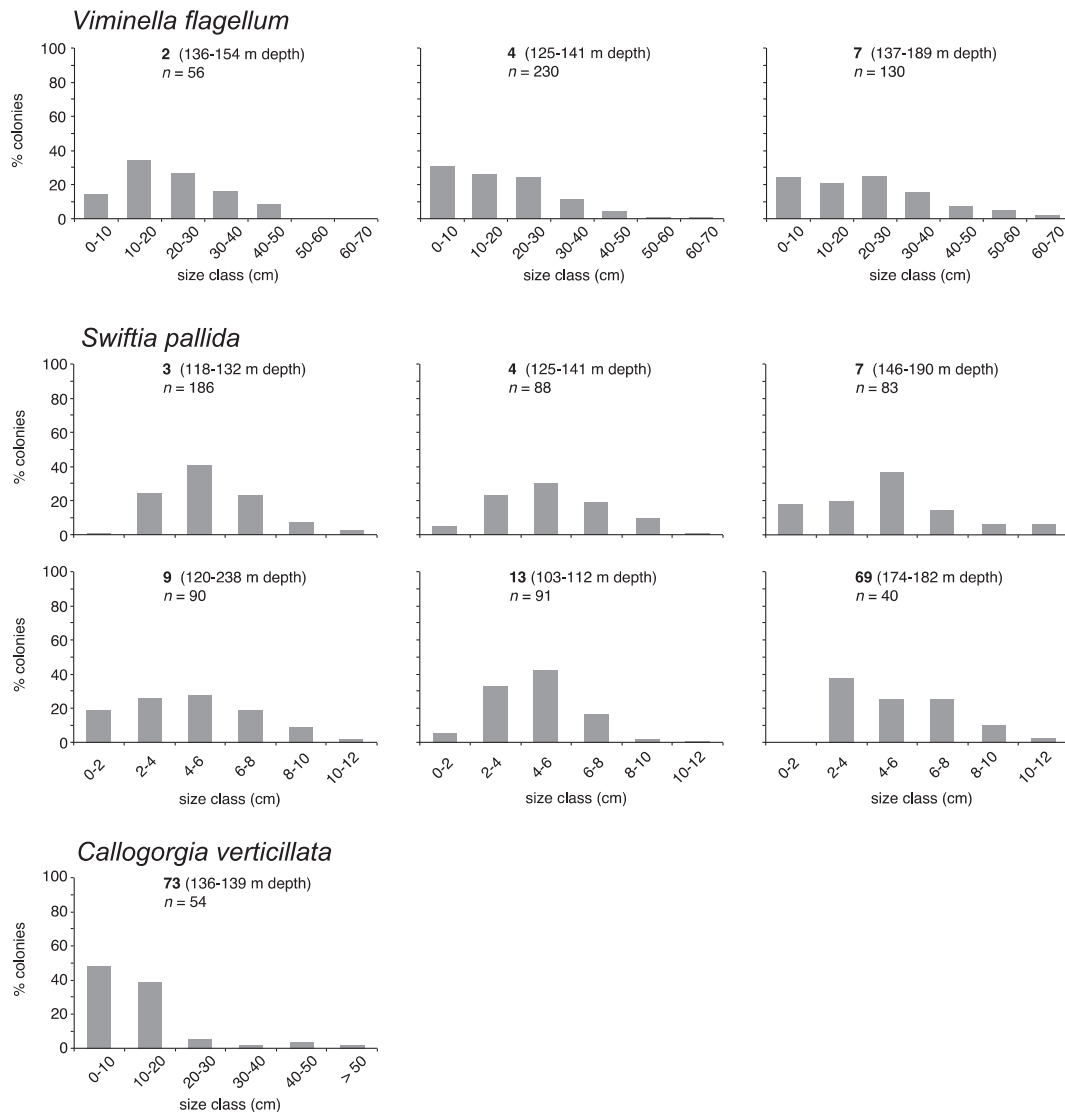


Fig. 6b. *V. flagellum*, *S. pallida* and *C. verticillata* population size frequency distribution (transect number as in Fig. 1 and Table 3, depth range, n = number of colonies).

3.5. Spatial structure

Spatial structure of gorgonian distribution was analyzed along three of the video transects (Fig. 8), representative of the continental shelf (transect 30) and slope (transects 4 and 6). On the continental shelf, *E. singularis* was positively associated with *P. macrospina* M1 at large spatial scales (more than 30 m), whereas they were independently distributed at smaller scales (Fig. 8, Table 4). *E. singularis* was negatively associated to *P. clavata* at small scales (less than 5 m) and tended to be independently distributed at large and intermediate scale. *P. clavata* was independently distributed with respect to *P. macrospina* at all scales (Fig. 8 and Table 4). On the continental slope, in transect 4, all species were independently distributed at small and medium scales (few to tens of meters) (Fig. 8 and Table 4). At larger spatial scales (more than 30 m), *C. verticillata*, *S. pallida* and *E. cavolinii* were positively associated, whereas *V. flagellum* occurred in exclusion to the other species (Fig. 8, Table 4). In transect 6, *E. cavolinii*, *P. macrospina* M3, *V. flagellum* and *B. mollis* were positively associated at large spatial scales (more than 30 m) (Fig. 8 and Table 4). *A. hirsuta* tended to be independently distributed at small (less than 30 m) and large spatial scale (more than 30 m) (Fig. 8 and Table 4). *E.*

cavolinii presented no association with *B. mollis* and *V. flagellum*, and the same situation was found for *P. macrospina* M3 when compared to *A. hirsuta*.

4. Discussion

The diversity of the studied deep gorgonian assemblages was much higher than in shallow Mediterranean coastal areas (Weinberg, 1978; Linares et al., 2008; Gori et al., 2011a). Nine species were observed to dwell between 40 and 360 m depth within the study area, while only 4–5 species are commonly present in littoral areas (Velimirov, 1973; Gori et al., 2011a; Garrabou et al., 2001). Gorgonian diversity resembled that reported of Atlantic coastal areas (Cúrdia et al., 2013), subtropical areas (Opresko, 1973) and similar depth ranges in the Aleutian Islands (Stone, 2006), compared to Mediterranean coastal bottoms (Gori et al., 2011a). Conversely, gorgonian density observed in these deep multispecific assemblages reached high values (~ 20 colonies m^{-2}) comparable to those reported for Mediterranean coastal species (Weinbauer and Velimirov, 1996; Linares et al., 2008; Gori et al., 2011a). These high density values are similar to those found in

Table 3
Size structure characteristics of the studied morphotypes and species: colony height, skewness and kurtosis. Significant skewness or kurtosis are indicated with one (p -value < 0.05) two (p -value < 0.01), or three asterisks (p -value < 0.001).

	Transect	Colonies	Height (cm)			Skewness			Kurtosis		
			Mean	SD	Max	Skew	p -value	Sig.	Kurt	p -value	Sig.
<i>E. singularis</i>	37	169	25.30	10.35	55.1	0.541	0.062		2.708	0.497	
	47	45	8.86	4.58	23	0.066	0.209		3.216	0.449	
<i>P. macrospina</i> (M1)	28	98	6.26	5.83	29.4	1.775	<0.001	***	5.870	<0.001	***
	29	81	5.90	3.36	18.4	1.377	0.004	**	4.939	0.008	**
	30	1099	8.72	6.90	33.1	1.056	<0.001	***	3.335	0.037	*
	37	65	10.82	6.10	33.8	0.829	0.075		4.550	0.027	*
	38	276	8.24	6.17	41.9	2.013	<0.001	***	7.596	<0.001	***
	43	251	12.10	6.24	29.4	0.185	0.421		2.247	<0.001	***
<i>P. macrospina</i> (M2)	28	461	6.82	5.13	30.1	1.302	<0.001	***	4.415	<0.001	***
	42	166	15.05	5.75	31.35	0.346	0.222		2.570	0.222	
	43	57	14.52	5.61	25.1	-0.242	0.590		2.366	0.286	
<i>P. macrospina</i> (M3)	2	70	17.22	9.07	41.31	0.784	0.086		2.831	0.967	
	3	52	17.95	11.43	55.65	13.566	0.018	*	4.037	0.272	
<i>E. cavolinii</i>	2	206	10.55	7.43	35.63	0.985	<0.001	***	3.205	0.417	
	3	384	15.16	10.06	50.45	0.739	<0.001	***	2.912	0.843	
	4	78	16.03	7.98	43.51	0.081	0.059		3.621	0.177	
	6	156	14.59	8.77	47.15	0.579	0.056		2.909	0.990	
	7	82	13.03	6.65	31.94	0.694	0.092		3.136	0.542	
	10	63	19.07	9.83	47.65	0.276	0.524		2.775	0.950	
	11	207	9.08	7.30	38.55	1.492	<0.001	***	4.940	<0.001	***
	13	110	11.93	6.93	29.75	0.442	0.202		2.468	0.198	
	22	71	9.81	4.92	22.42	0.686	0.116		2.703	0.785	
	<i>V. flagellum</i>	2	56	42.35	22.20	96.41	0.308	0.500		2.558	0.606
4		230	38.19	25.14	148.3	1.045	<0.001	***	4.721	<0.001	***
7		130	46.00	30.86	136.6	0.740	0.0300	*	3.045	0.689	
<i>C. verticillata</i>	73	54	26.43	21.52	115.3	2.513	<0.001	***	9.467	<0.001	***
<i>S. pallida</i>	3	186	5.35	1.98	13.54	0.932	<0.001	***	4.452	<0.001	***
	4	88	7.12	2.12	12.17	0.224	0.548		2.655	0.615	
	7	83	6.83	2.71	13.96	0.753	0.069		3.190	0.480	
	9	90	6.66	2.81	17.46	1.061	0.013	*	5.329	0.002	**
	13	91	4.62	1.75	10.47	0.552	0.151		3.641	0.156	
	69	40	5.32	1.99	10.39	0.439	0.408		2.571	0.759	

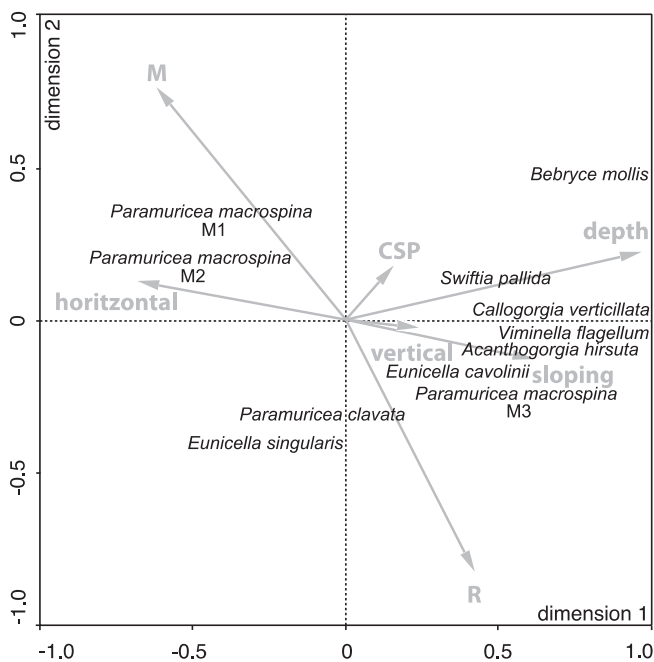
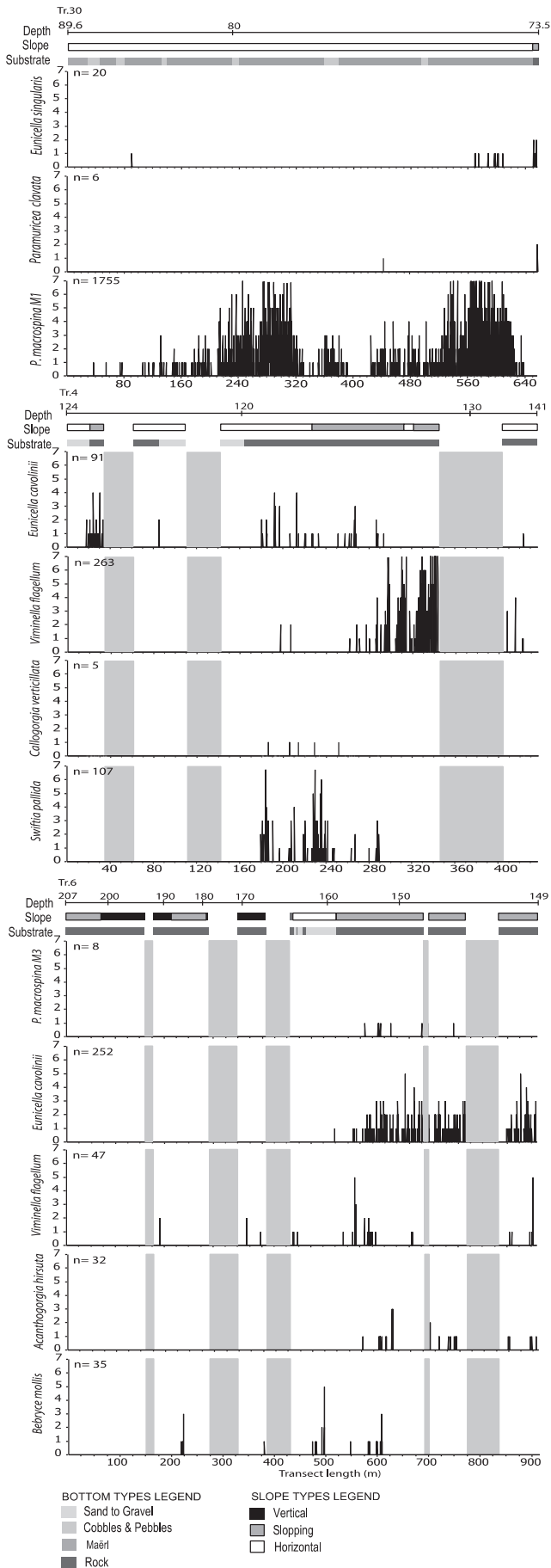


Fig. 7. Canonical correspondence analysis (CCA): biplot showing the ordination of gorgonian species and the roles of the significant environmental variables. M: maërl, CSP: cobbles and pebbles and R: rocky substrates.

temperate (Grigg, 1975, 1977; Cúrdia et al., 2013) and tropical (Lasker and Coffroth, 1983; Yoshioka and Yoshioka, 1989) coastal gorgonian assemblages, and clearly exceed those found at similar depths (180–500 m) in the North Atlantic (Mortensen and Buhl-Mortensen, 2004; Buhl-Mortensen et al., 2014), and polar continental shelves and slopes (Orejas et al., 2002; Müller et al., 2012).

However, the observed high gorgonian diversity was mainly concentrated on the shelf edge (100–180 m depth). A clear vertical zonation can be established regarding species distribution: (1) coastal species extending their distribution to deep coralligenous banks (*E. singularis* and *P. clavata*); (2) dominance of one single species on the continental shelf (*P. macrospina*); (3) concentration of several gorgonian species on the shelf edge (*E. cavolinii*, *P. macrospina*, *S. pallida*, *A. hirsuta*, *V. flagellum*, *B. mollis* and *C. verticillata*); and (4) species extending their distribution deeper into the upper slope (*B. mollis*, *C. verticillata*, *V. flagellum* and *S. pallida*).

The common Mediterranean coastal species *E. singularis* and *P. clavata* were found on deep coralligenous banks on the continental shelf of the studied area (45–100 m depth). The high water transparency allows a very deep distribution of coralligenous banks (Ballesteros and Zabala, 1993), which in turns could explain the deep distribution of *E. singularis* within the study area (down to 100 m depth). In coastal environments characterized by high water turbidity, this species is limited to 70 m depth (Gori et al., 2011a). In the study area continental shelf both species' density was much lower than that reported in shallow coastal environments (Linares et al., 2008; Gori et al., 2011a). This could indicate that these species' deep bathymetric limit lies around this depth, according to our data. Interestingly, the observed colonies of *E. singularis* pre-



sented the same morphology as the deep asymbiotic morphotype reported in coastal environments below 40 m depth (Théodor, 1969; Gori et al., 2012). These populations were dominated by medium sized colonies, corresponding to what has been observed in deep coastal environments (60 m depth) (Gori et al., 2011b). Conversely, in shallow coastal environments (20 m depth) these species populations are mainly composed of small colonies (Linares et al., 2008). Populations of *P. clavata* extending beyond 40 m have also been reported in several coastal areas (Gori et al., 2011a; Angiolillo et al., 2015), as well as on top of seamounts (Bo et al., 2011) and on rocky bottoms of the continental shelf and slope (Bo et al., 2012, 2014). In these deep environments, *P. clavata* colonies generally achieve larger sizes (50 ± 15 cm (mean \pm SD), min = 25 cm, max = 90 cm) than in shallower environments (Linares et al., 2008), as a possible consequence of the higher environmental stability of deeper areas (Grigg, 1975). Deep populations of *E. singularis* and *P. clavata* are probably protected from high hydrodynamic processes (Teixidó et al., 2013) as well as from unusually high-temperature conditions associated to mass mortality events in shallow benthic communities (Garrabou et al., 2009).

Maërl beds on the continental shelf of the studied area are covered by very high abundances of *P. macrospina* (M1 and M2) (Supplementary material 3). In this environment this species presents high frequency of occurrence over large areas (Fig. 4 and 8) and can reach densities of up to 33 colonies m^{-2} , which is at odds with previous data on this species, having been only reported on rocky substrates and never as a dominant species (Bo et al., 2011; Topçu and Öztürk, 2015). Preservation of these *P. macrospina* populations may be a consequence of low trawling pressure over large areas of the continental shelf (Moranta et al., 2014), as well as the habit of local artisanal fishermen to clean their nets *in situ* (Díaz et al., 2015). This habit consists of releasing by-catch over the same fishing grounds. This practice might result in partial damage of entangled colonies of *P. macrospina*, but as long as their holdfast remains attached to the maërl rodholite, their survival might be favored (Díaz et al., 2015). Population size structures of *P. macrospina* were mostly asymmetrical and positively skewed (Table 4), suggesting high recruitment rates (Linares et al., 2008) and implying that maërl beds are particularly suitable habitats for this species. However, unlike *E. singularis* and *P. clavata* that occur on coralligenous banks, the structural instability of maërl may limit the presence of large colonies of *P. macrospina* in the continental shelf (Tunncliffe and James, 1983). Furthermore, fishing activities might be particularly detrimental to large colonies, which are probably more susceptible than smaller colonies to get entangled and broken by nets used by artisanal fishermen in the area. Indeed, populations dominated by small colonies have been reported in intensely fished areas (Althaus et al., 2009).

Highest gorgonian diversity was concentrated on the rocky bottoms of the shelf edge (at 100–180 m depth). In this environment, gorgonian assemblages were mostly multispecific (92% of occupied sampling units contained several species) (Supplementary material 4) and included seven of the nine observed species (Fig. 4 and 5). This diversity is probably influenced by the joint effect of habitat heterogeneity and hydrodynamic stability. In the study area's shelf edge, boulders, slaps and vertical walls alternate over short distances. Shelf edge are mainly influenced by steady flow currents and stable hydrodynamic conditions (e.g. Puig et al., 2000), such as the Balearic current associated with the Balearic front, which

Fig. 8. Density plots. Species densities are plotted along representative transects from the continental shelf (transect 30) continental shelf edge and slope (transect 4 and 6, respectively). Bottom type and seabed slope are indicated (see legend). Vertical gray rectangles indicate invalid sequences for the analysis (Tr = transect, n = number of colonies).

Table 4
Summary of the three-term local quadrat covariance (3TLQC). The scale (m) of any positive or negative associations between distributions of each pair of species is indicated.

Transect number	Compared species	Negative	Random	Positive
30	<i>P. macrospina</i> M1 vs. <i>E. singularis</i>		0–30 // 55–75	30–55 // >75
	<i>P. macrospina</i> M1 vs. <i>P. clavata</i>			All transect
	<i>P. clavata</i> vs. <i>E. singularis</i>	2–5	>5	
4	<i>C. verticillata</i> vs. <i>E. cavolinii</i>		0–50	>50
	<i>C. verticillata</i> vs. <i>S. pallida</i>		0–5	>5
	<i>C. verticillata</i> vs. <i>V. flagellum</i>	>55	0–55	
	<i>E. cavolinii</i> vs. <i>S. pallida</i>		0–50	>50
	<i>E. cavolinii</i> vs. <i>V. flagellum</i>	>34	0–34	
	<i>S. pallida</i> vs. <i>V. flagellum</i>	>48	0–48	
6	<i>A. hirsuta</i> vs. <i>B. mollis</i>	30–60	0–30 // >60	
	<i>A. hirsuta</i> vs. <i>E. cavolinii</i>	11–20	0–11 // 20–40	>40
	<i>A. hirsuta</i> vs. <i>P. macrospina</i> M3		All transect	
	<i>A. hirsuta</i> vs. <i>V. flagellum</i>	30–65	0–30 // >65	
	<i>B. mollis</i> vs. <i>E. cavolinii</i>		All transect	
	<i>B. mollis</i> vs. <i>P. macrospina</i> M3		20–30	0–20 // >30
	<i>B. mollis</i> vs. <i>V. flagellum</i>	11–20	0–11 // 20–32	>32
	<i>E. cavolinii</i> vs. <i>P. macrospina</i> M3		0–35	>35
	<i>E. cavolinii</i> vs. <i>V. flagellum</i>		All transect	
	<i>P. macrospina</i> M3 vs. <i>V. flagellum</i>	12–22	0–12 // 22–60	>60

flows from south to north along the western shelf edge of the Balearic Promontory (Ruiz et al., 2009). Stable hydrodynamic conditions, together with the hydrodynamic processes that increase particle suspension in the near-bottom water layers, may also suppose enhanced food availability for gorgonians on the shelf edge (Thiem et al., 2006). Finally, the observed increase in gorgonian diversity on the shelf edge could also result from the merging of species with shallower and deeper distributions, causing a mid-domain effect (Colwell and Lees, 2000), as previously suggested for deep coral diversity in other locations (Stone, 2006; Matsumoto et al., 2007). Most gorgonian populations located on the shelf edge had a bell-shaped, unimodal size structure dominated by medium sized colonies (Figs. 6a and 6b). *P. macrospina* (M3) populations on the shelf edge were bell-shaped, in contrast to its populations on the continental shelf (M1 and M2) that were mostly dominated by small size colonies. When compared to maërl, rocky substrates provide higher structural stability allowing colonies to achieve larger sizes. In these multispecific gorgonian assemblages of the shelf edge, the fine scale spatial covariance of species appears to be related to the combined effect of density, occupancy, and colony size. When a large species such as *V. flagellum* achieves high-densities over extended areas, it tends to exclude any other species (Fig. 8). Conversely, coexistence is observed at low and intermediate densities among large (*C. verticillata*), medium (*E. cavolinii*) and small sized species (*S. pallida*). This could indicate that differences in size may reduce interspecific competition for space and food (Schoener, 1974). Species with similar size probably feed on the food particles that are transported by the same water layer, with a potential competition for food (Kim and Lasker, 1997). Conversely, species with different size are probably feeding on different water layer, thus avoiding potential shading processes. Coexistence at medium spatial scales (~30 m) may also occur at low and intermediate densities among species of similar size and morphology (*E. cavolinii* and *A. hirsuta*). In this case, however, spatial exclusion occurred at smaller scales (~10 m), suggesting that these species share the same habitat but partially compete for space. Overall, the species dwelling on the shelf edge within the study area, have been recently found with increasing frequency on rocky substrates at similar depths in other areas of the Mediterranean Sea (Bo et al., 2009, 2011, 2012, 2014), suggesting the general validity of the observed pattern of high gorgonian diversity.

Below the shelf edge, gorgonian abundance strongly decreases, and only *B. mollis*, *S. pallida*, *V. flagellum* and *C. verticillata* were observed to extend their distribution under 200 m depth (Fig. 4). Gorgonian assemblages are here mainly monospecific, (76% of occupied sampling units contained one single species) and with low densities ($\sim 0.75 \pm 0.3$ colonies m^{-2} (mean \pm SD)) (Supplementary material 5). These species are typically found along the continental slope in other Mediterranean locations (Mytilineou et al., 2014; Deidun et al., 2014; Bo et al., 2015) where they mostly concentrate along the edges, maximizing their exposure to currents (Genin et al., 1986). On the scarce rocky substrates occurring in these deeper environments, gorgonian abundance tends to decrease with increasing depth, and antipatharians become the dominant arborescent species (Deidun et al., 2014; Bo et al., 2015). Finally, the soft sediments of these deeper environments can be colonized by the bamboo coral *Isidella elongata* (Maynou and Cartes, 2012; Bo et al., 2015), which can form extended assemblages in bathyal muds (Pérès, 1967).

Due to their arborescent morphology, gorgonians are especially vulnerable to fishing activities (Mytilineou et al., 2014; Bo et al., 2014), and their slow growth rate (Coma et al., 1998; Sherwood and Edinger, 2009) makes their recovery from related fishing damages very slow (Althaus et al., 2009). The high diversity and abundance of deep gorgonian assemblages in the rocky areas of the shelf edge, and the vast area covered by high densities of *P. macrospina* on the continental shelf are probably related to the low trawling pressure and the exceptional fishing practices exerted by local artisanal fishermen. This represents an example of the possibility of conserving deep gorgonian assemblages and their associated high-diverse fauna (e.g. Buhl-Mortensen and Mortensen, 2005) through better management of fishing activities. These high-density deep gorgonian assemblages may provide an approximate idea of how Mediterranean continental shelves and upper slopes stood before decades of bottom trawling.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.pocan.2016.05.001>.

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