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Sponge assemblages on the deep Mediterranean continental shelf and slope (Menorca Channel, Western Mediterranean Sea)



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A B S T R A C T

Sponge assemblages on continental shelves and slopes around the world have been known about for centuries. However, due to limitations of the traditional sampling systems, data about individual sponge species rather than assemblages have been reported. This study characterizes sponge assemblages over a wide bathymetric range (~50–350 m depth) and covering the entire continental shelf and the upper slope of the Menorca Channel, an area soon to be declared a Marine Protected Area (MPA) as part of the Natura 2000 Network. Quantitative analysis of 85 video-transects (a total linear distance of 75 km), together with representative collections to confirm species identifications, allowed us to discriminate six major assemblages. Differences in the assemblages mainly corresponded to differences in substrate type and depth. On the inner continental shelf, a semi-sciaphilous Axinellid assemblage dominated the rocky outcrops. Maërl beds on the inner continental shelf were dominated by *Haliclona (Reniera) mediterranea*, whereas the horny sponge *Aplysina cavernicola* and several other haliclionids mostly dominated maërl beds and rocky substrates of the outer shelf. Soft sediments on the shelf break hosted a monospecific *Thenea muricata* assemblage, whereas rocky substrates of the shelf break were characterized by a mixture of encrusting, columnar and fan-shaped sponges. Finally, the upper slope was dominated by *Hamacantha (Vomerula) falcula* and the hexactinellid *Tretodictyum reisi*. Overall, sponge diversity showed its highest values above the shelf break, plummeting severely on the upper slope. Despite this diversity decrease, we found very high densities (> 70 ind./m²) of sponges over vast areas of both the shelf break and the upper slope.

1. Introduction

Sponges play a significant role in the functioning of marine benthic ecosystems, (Gili and Coma, 1998; Van Soest et al., 2012), where some of them are key bioengineering species (Rützler, 1975; Wulff and Buss, 1979; Buhl-Mortensen et al., 2010) thanks to their three-dimensional structures and long lifespans (McMurray et al., 2010). Sponges can modify environmental properties and provide suitable habitats for a wide variety of other marine species (Van Soest, 2007; Bell, 2008), from bacteria to commercial fishes (Buhl-Mortensen et al., 2010; Hogg et al., 2010; Van Soest et al., 2012). Sponge assemblages dominate several, distinctive, hard-bottom environments (Lissner et al., 1986), being one of the most important structural organisms at several locations around the world (e.g. Indo-Pacific, Bell and Smith, 2004; Atlantic, Hogg et al., 2010; Antarctica, Göcke and Janussen, 2013; Mediterranean Sea, Bertolino et al., 2015; Caribbean Sea, Maldonado et al., 2016).

In general terms, sponge assemblages show a high variability in their species composition across different environments, with diversity values that tend to increase with depth in littoral habitats (Roberts and Davis, 1996; Bell and Smith, 2004). Nonetheless, this pattern has barely been studied in areas beyond SCUBA depth range (> 60 m) (Vacelet, 1969; Bourny-Esnault, 1971; Vacelet et al., 1994), and sponge assemblages of the continental shelf and slope have been explored with less intensity. Although the Mediterranean sponge fauna is among the world's most studied (Van Soest et al., 2012), information is minimal for sponges from Mediterranean deep-sea areas compared to shallow waters (Bo et al., 2012), with most of the data deriving from indirect sampling methods (Vacelet, 1969; Voultsiadou, 2005) or from by-catch specimens collected by bottom trawlers.

Recent technological developments and increased availability of towed video equipment, remotely operated vehicles (ROVs), manned submersibles and autonomous underwater vehicles (AUVs) have

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significantly increased our access to deep environments (Longo et al., 2005; Bo et al., 2015; Maldonado et al., 2016; Pierdomenico, 2016; Pineda et al., 2016). Most studies based on these technologies, however, have been conducted below 150 m depth, leaving intermediate depths relatively unexplored. Moreover, most studies have focused on anthozoan species (Longo et al., 2005; Danovaro et al., 2010; Buhl-Mortensen and Buhl-Mortensen, 2014), and only a few have focused on sponge assemblages (Bo et al., 2012; Bertolino et al., 2013, 2015). Novel work has revealed the presence of highly diverse sponge assemblages on the continental shelf of the Mediterranean Sea (Pedel and Fabri, 2011; Bertolino et al., 2015). Nevertheless, these areas have been intensely impacted by fishing practices, especially bottom trawling and long line fishing, which have decimated their sponge assemblages (Pansini and Musso, 1991; Pronzato, 2003). Consequently, relatively well preserved benthic communities are mostly confined to locations not frequented by bottom trawlers (Bo et al., 2015), generally thanks to outcropping rocks that would damage trawl nets (Díaz et al., 2015). As for the continental shelf and slope of the Menorca Channel, trawling pressure during the past decades has mainly been restricted to a few locations, leaving large areas relatively unimpacted (Grinyó, 2016). This area will soon be declared a Marine Protected Area under the Natura 2000 network; thus, a detailed characterization of the species and assemblages currently present on its bottoms is required to provide tools for management and as baselines for monitoring changes in its diversity in coming years.

The current study aims to: (i) determine the best size of sampling unit to study sponge assemblages on the Balearic continental shelf and upper slope, (ii) characterize the sponge assemblages in deep habitats of the continental shelf and upper slope in the Menorca Channel and (iii) evaluate the variation of sponge diversity with depth.

2. Material and methods

2.1. Study area

The Menorca Channel is located between Mallorca and Menorca Islands ($39^{\circ}53'0.73''\text{N}$, $3^{\circ}29'51.16''\text{E}$) (Fig. 1) in the Balearic Archipelago (western Mediterranean Sea), and is part of the Balearic Promontory (Acosta et al., 2002). The Channel's continental shelf extends between 40 and ~ 110 m depth, and mainly consists of maërl substrates of varying densities, alternating with patches of coastal detrital sediments and coralligenous outcrops (Barberá et al., 2012). Deeper, distinctively smooth relief and large extents of detrital sediments and fine sand with a few isolated patches of outcropping rock characterize most of the continental shelf break and continental slope at 150–350 m depth (Grinyó, 2016). Vertical walls and rock outcrops are the dominant substrate near Cap Formentor (Fig. 1a) and in the Menorca Canyon's head (Fig. 1b). Hydrologically, the Menorca Channel is located in a border zone between the Balearic and the Algerian sub-basins. The northern part of the study area is mainly influenced by a branch of the Liguro-Provençal-Catalan current (also termed the Northern Current), known as the Balearic Current (Balbín et al., 2012) and its associated front (Ruiz et al., 2009). The Balearic Current flows over the northern slope of the Balearic archipelago at ~ 200 m depth (López García et al., 1994; Ruiz et al., 2009). The southern slope is not influenced by a steady current (Amores and Monserrat, 2014), but mesoscale gyres arrive intermittently after detaching from the Algerian Current and the Almería-Oran front (Millot, 1987).

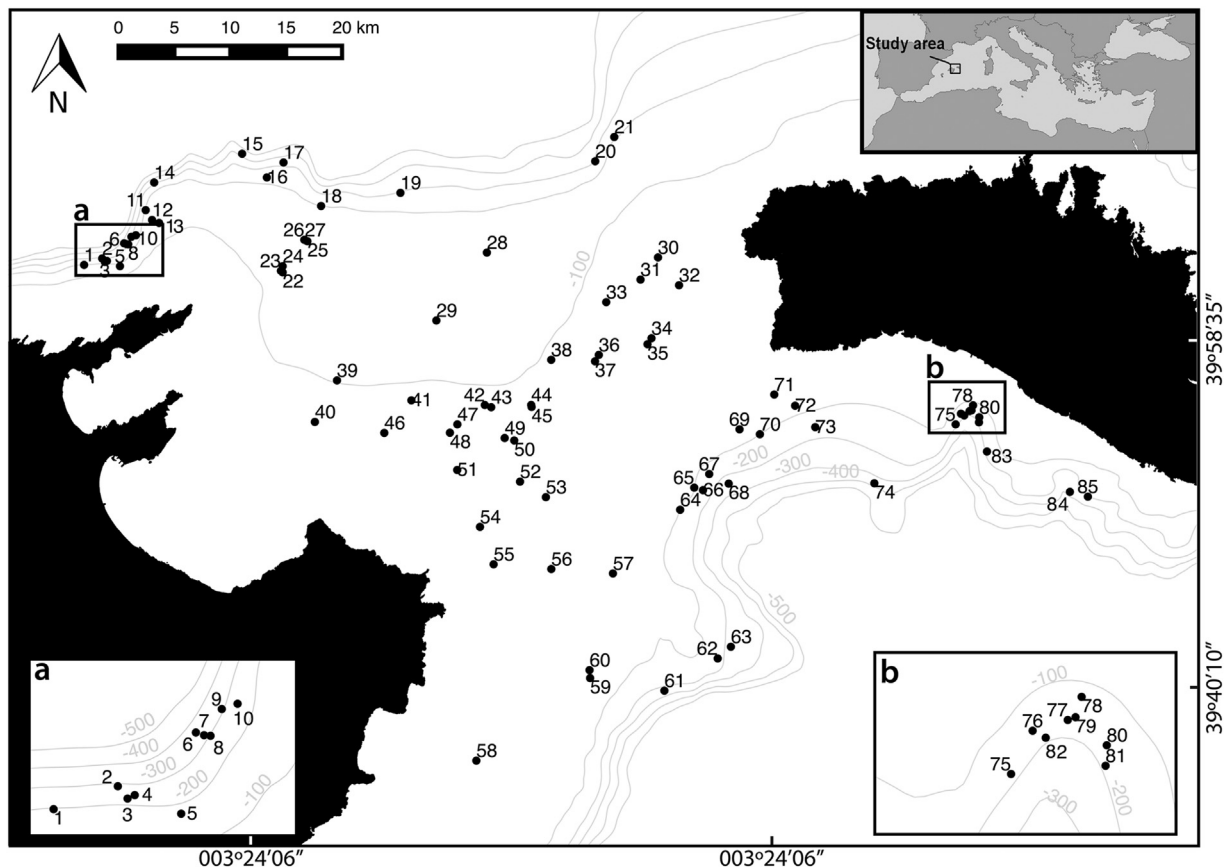


Fig. 1. Location of the video transects in the study area. (a) Enlargement showing video tracks 1–10 in Cap Formentor. (b) Enlargement showing video tracks 75–82 in the Menorca Canyon's head. The location of the survey area in the Mediterranean Sea is shown in the upper right corner. Projected view (UTM Zone 31N (WGS84) with geographic (WGS84) coordinates indicated for reference.

2.2. Video recording

Eighty-five video transects, covering a total distance of 75 km, were recorded between 50 and 350 m depth during six different surveys in the frame of the LIFE + INDEMARES and ENPI-ECOSAFIMED projects on board the R/V “García del Cid” (September 2010, April 2011, October 2011, June 2012), the R/V “Miguel Oliver” (August 2011) and the R/V “SOCIB” (August 2014) (Fig. 1; Supplementary material 1). The first 20 video transects during the first two surveys were recorded with the manned submersible JAGO (IFM-GEOMAR), whereas the remaining 65 video transects were recorded during the last four surveys using the ROV Nemo, operated by Gavin Newman. Both vehicles were equipped with depth sensors, a grabber and an HD camera (1920 × 1080) that recorded images in a digital format. Two parallel laser beams provided scales on the images, which were required for the spatial-density analyses. Both JAGO and Nemo moved at a constant speed of ~0.3 knots, with transect lengths ranging between 80 and 2375 m. Transects were haphazardly set along the study area in order to cover as much of its extension as possible, with areas suspected to be dominated by rocky substrates explored more intensively (Fig. 1; Supplementary material 1).

In order to confirm the taxonomic identifications of the species observed in the video footage, individuals were collected along several transects and preserved for morphologic analyses using 10% formalin in seawater. Additionally, a small tissue sample from each individual was preserved in absolute ethanol for genetic determination.

2.3. Video analysis

Quantitative video analysis followed the methodology described in Gori et al. (2011), Ambroso et al. (2013) and Grinyó et al. (2016), using the software Final Cut Pro 7 (Apple Inc.). Pauses and loops were removed from the footage to avoid overestimation of transect length. Video sequences recorded too far above the seafloor or with poor image quality were discarded from the analysis. The remaining video footage was considered suitable for analysis (93.4%, linear distance of 70 km). Every sponge observed within the laser beams (marking a width of 0.3 m) as the vehicle cruised over the seabed was annotated and assigned a time reference, this being the time elapsed since the beginning of the video transect. A similar procedure was used to characterize substrate type, depth and slope along each transect. Seabed substrate types were classified in four categories based on the Wentworth scale (Wentworth, 1922): sands, cobbles and pebbles, maërl, and outcropping rock. Seabed slope was classified as horizontal (0–30°), sloping (30–80°) or vertical (80–90°). Slopes were estimated from the video and the depth sensor. Depth was recorded as the time reference of any 0.1 m depth change. Time references were transformed into distances (d) from the beginning of the video transect according to the vehicles speed ($d = t \cdot v$, where t is the time reference expressed in seconds, and v is the velocity expressed in meters per second).

2.4. Species identification

Species identifications were carried out on collected individuals and HD images from the video transects using previous taxonomic studies on Atlantic-Mediterranean and Balearic sponge faunas (e.g., Uriz, 1986; Bibiloni, 1990; Hooper and Van Soest, 2002). Whenever possible, close-up images of relevant parts of the sponges (e.g. inhalant/exhalant structures, surface patterns) were recorded to help in species identifications. Sponges were identified to the lowest possible taxonomic level.

2.5. Data analysis

2.5.1. Determination of sampling units

In order to determine the minimal areas necessary to adequately characterize communities, we calculated a species-area curve as suggested by Weinberg (1978). A species-area curve is drawn by assessing the number of species present in a first quadrat of a given area, then

doubling that surface and recounting the species present, and then enlarging the sample successively. Initially, the species area-curves tend to rise sharply until reaching a break point, after which they approach to a stable asymptote. The area at that point is assumed to be the minimal area characterizing the sampled community. In order to obtain an objective estimate of the asymptotic value, several approaches have been given (Cain and Castro, 1959; Weinberg, 1978). We selected Weinberg's (1978) stabilization criterion, that is, the minimal community-defining area is reached when doubling the sample area results in an increase of less than 10% in the number of species counted. This criterion was favored as it fits better than others for marine invertebrate communities (Weinberg, 1978).

This species-area analysis is of key importance for the later statistical analyses and hence is detailed here. Raw analyzed video data were transformed into a matrix of 1 m² samples in which all sponge individuals were considered. Species-area curves were generated with R software (R Development Core Team, 2014) by means of the function *specaccum* in the *vegan* package (Oksanen et al., 2016).

The minimal area for the study of sponge assemblages in the Menorca Channel was selected as 20 m² (Fig. 2).

2.5.2. Sponge occupancy and assemblage composition

For statistical analysis, transects were divided into strings of adjacent 20 m² sampling units (0.3 m width and 66.66 m long), adding to a total of 926 sampling units. For all sampling units, the numbers of individuals of each identified species were tabulated. Sponge species were then evaluated according to occurrence (frequency of appearance of each species in the set of sampling units), abundance (number of individuals per sampling unit) and density (ind./m²).

To explore the possible assemblages present, the sponge species abundance data were square-root transformed and distances between pairs of samples were calculated using the Bray-Curtis dissimilarity index. The dissimilarity matrix was then represented as a dendrogram using the *hclust* function of the R *vegan* package, and groups were determined using a 20% similarity threshold. To determine the statistical significance of differences among groups, an ANOSIM test was run using the *anosim* function of the *vegan* package. Additionally, a SIMPER analysis (Similarity Percentage; Clarke and Warwick, 1994) was performed to identify the species contributing most to the dissimilarities

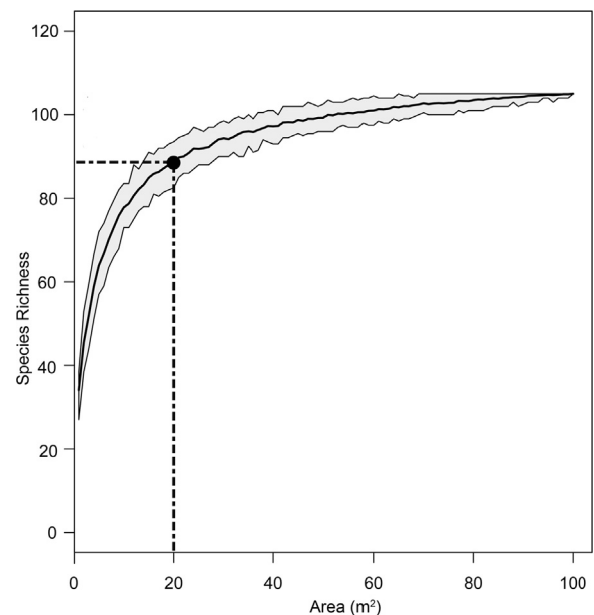


Fig. 2. Species-area curve for sponge assemblages in the Menorca Channel. Black line represents the mean species richness, whereas the grey area represents the 95% confidence interval. Dot-dashed lines and the dot at their intersection mark the threshold where the minimal assemblage defining area is reached.

among assemblages. That was done using PRIMER v6 software (Clarke and Warwick, 2001).

2.5.3. Relationships with environmental parameters

The environmental factors determining sponge assemblage composition were explored by canonical correspondence analysis (CCA), with species abundances square-root transformed. CCA is a constrained multivariate ordination technique for identifying possible relationships between species composition (response variables) and their habitat (explanatory variables) (Ter Braak, 1994; Greenacre, 2013). The environmental variables used in our CCA were depth, slope and substrate type. Depth was coded into five fuzzy categories that reduce the information contained onto a categorical scale (Greenacre, 2013). The fuzzy-coding approach allows for a more accurate depiction of non-linear relationships among environmental data and biological gradients, as well as improving the explained variance (Greenacre, 2013). Since the inclusion of rare or sporadic species in multivariate analyses might constrain or cause distortions in the final results (Marchant, 2002; Poos and Jackson, 2012), sponge species observed less than 5 times were excluded from the CCA analysis, as were sampling units without sponges. As a result, the CCA was conducted on a reduced dataset of 380 sampling units which contained 87 sponge taxa.

2.5.4. Variation of sponge diversity with depth

Sponge species richness or beta-diversity was compared among the continental shelf (50–110 m depth), shelf break (110–180 m depth) and the upper slope (180–350 m depth) by evaluating the slopes of randomized species accumulation curves (Ugland et al., 2003) with the *speaccum* function of the *vegan* package. Mean species accumulation curves and their standard deviation from random permutations of data ($n = 100$) give an estimate of the rate at which new species are encountered as sampling effort increases (Vetter et al., 2010; De Leo et al., 2014), avoiding the distortions due to variations in species abundance or sampling effort (Gotelli and Colwell, 2001).

Sponge species richness and diversity (quantified by means of the exponent of Shannon's diversity index) were also computed at a finer scale of 20 m depth intervals over the studied depth gradient (50–350 m depth). The exponent of Shannon's information entropy was preferred over other diversity indices (e.g. Shannon's entropy or the Simpson index) because it weights all species by their frequency without favouring either rarest or most common species (Jost, 2006). Sampling effort was also evaluated based on the number of sampling units in each 20 m depth interval.

3. Results

3.1. Sponge diversity and assemblage composition

Sponges occurred in 76% of the 926 sampling units. A total of 40,523 sponge individuals were recorded along all transects, from which 32,234 individuals could be identified at least to genus level (109 sponge taxa; species list given in Supplementary material 2). Sponges belonging to the classes Calcarea, Demospongiae, Homoscleromorpha and Hexactinellida were identified in the video footage. Demospongiae represented more than 98.8% of all sponge individuals and was distributed along the whole bathymetric range. Calcarea and Homoscleromorpha were only present on the continental shelf, whereas Hexactinellida were limited to the upper slope.

Haliclona cf. *elegans* and *Rhabderemia* sp. were the most abundant and frequent species, each accounting for 20% of the observed sponge individuals, and they were present in 19% and 17.7% of the sampling units, respectively (Table 1). Beside these two species, the most frequent sponges were *Axinella damicornis*, *Dictyonella* sp. 1, *Haliclona mediterranea*, *Aplysina cavernicola*, *Poecillastra compressa*, *Axinella verrucosa*, *Hexadella* cf. *dedritifera* and *Hamacantha falcu*. The most abundant sponges, beside *H. cf. elegans* and *Rhabderemia* sp., were *A. cavernicola*, *H. mediterranea*, *H. falcu*, *A. damicornis*, *Haliclona implexa*, *Hamacantha* sp., *Haliclona* sp. 1, and *Dictyonella* sp. 1 (Table 1). The remaining species accounted individually for less than 2% of the overall observed sponge abundances (Supplementary material 2).

Cluster analysis separated six assemblages at a 20% similarity threshold, being significantly different from each other (ANOSIM, $p < 0.001$). Average similarity in species composition within assemblages ranged between 31% and 62% (Fig. 3; Table 2).

The *Thenea muricata* assemblage was monospecific, with only *T. muricata* individuals. The Axinellid assemblage was characterized by *A. damicornis* and *A. verrucosa*, contributing 85.5% and 9.6% of the total individuals present, respectively. The *Haliclona mediterranea* assemblage was characterized by *H. mediterranea* (82.7%), *Siphonochalina* sp. 2 (10.1%) and *Tethya aurantium* (3.3%). The “*Haliclonid-Aplysina*” assemblage was the most diverse, with the greatest number of species required to reach a 95% cumulative contribution: *H. cf. elegans* (52.5%), *H. mediterranea* (10.8%), *A. cavernicola* (5.8%), *A. damicornis* (4.7%), *Axinella* cf. *pseudominuta* (4.2%), *H. implexa* (4.1%), *Haliclona* sp. 1 (3.4%), *Haliclona* sp. 10 (2.8%), *Rhabderemia* sp. (1.9%), *Haliclona poecillastroides* (1.8%), *Haliclona fulva* (1.7%) and *Hamacantha* sp. (1.7%). The “*Rhabderemia-Dictyonella*” assemblage was characterized by *Rhabderemia* sp. (51.3%), *Dictyonella* sp. 1 (28.0%), *H. falcu* (5.6%), *P. compressa* (5.5%), *H. cf. dedritifera* (5.3%). Finally, the “*Hamacantha-Tretodictyum*” assemblage consisted of *H. falcu* (76.6%), *Tretodictyum reiswigi* (10.3%), *Haliclona mucosa* (6.6%) and *H. cf. dedritifera* (2.8%).

Table 1

Most abundant and frequent sponge species in the study area. Occupancy (frequency of occurrence in the set of sampling units), abundance (number of individuals), mean and maximum density and bathymetric range are given for each species.

Species	Sampling units		N° individuals		Mean density ± SD	Max. density	Depth-range m
	Number	(%)	Number	(%)	Individuals/m ²	Individuals/m ²	
<i>A. cavernicola</i>	105	(11.33)	3882	(12)	5 ± 4.9	53	72–179
<i>A. damicornis</i>	131	(14.14)	1555	(4.8)	2.4 ± 2.5	20	52–100
<i>A. verrucosa</i>	85	(9.2)	583	(1.8)	2.2 ± 2.2	18	52–100
<i>Dictyonella</i> sp. 1	128	(13.82)	1075	(3.3)	2 ± 1.4	8	92–246
<i>Haliclona</i> sp. 1	66	(7.1)	1149	(3.7)	2.8 ± 2.9	26	75–113
<i>H. cf. elegans</i>	176	(19)	6481	(20.1)	5.3 ± 6.8	71	61–116
<i>H. implexa</i>	66	(7.1)	1414	(4.4)	5 ± 6.4	45	73–110
<i>H. mediterranea</i>	119	(12.85)	1799	(5.6)	2.6 ± 2.8	25	60–110
<i>Hamacantha</i> sp.	51	(5.5)	1204	(3.6)	2.8 ± 2.3	14	95–174
<i>H. falcu</i>	83	(9)	1557	(4.8)	3.4 ± 3	17	102–346
<i>H. cf. dedritifera</i>	85	(9.2)	447	(1.8)	2 ± 2.3	18	86–321
<i>P. compressa</i>	88	(9.5)	282	(0.9)	1.3 ± 0.8	10	95–246
<i>Rhabderemia</i> sp.	164	(17.7)	6509	(20.2)	6.2 ± 6.5	43	72–228

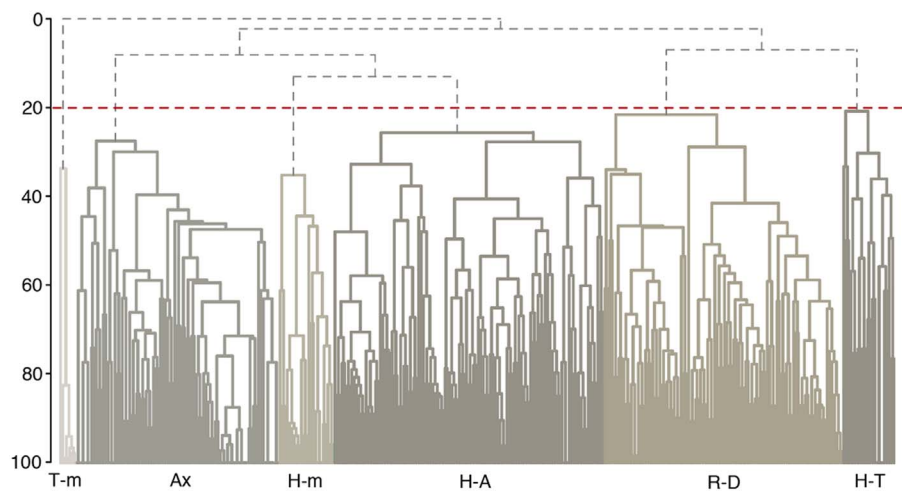


Fig. 3. Dendrogram representing the sample clustering based on a Bray-Curtis dissimilarity matrix. Red-dashed line represents a 20% similarity threshold. Groups are differently shaded on a grey-scale to ease visual group identification. Assemblages are labeled as follows: Axinellids (Ax); *Haliclona mediterranea* (H-m); “Haliclonid-Aplysina” (H-A); *Thena muricata* (T-m); “*Rhabderemia-Diclyonella*” (R-D); “*Hamacantha-Tretodictyum*” (H-T).

Table 2
SIMPER analysis. Species that constitute up to 95% of cumulative contribution of each similarity group are present. The average similarity values were as follows: *Thena muricata* = 45.63%; Axinellids = 61.69%, *Haliclona mediterranea* = 43.41%, “Haliclonid-Aplysina” = 51.75%; “*Rhabderemia-Diclyonella*” = 31.21%; “*Hamacantha-Tretodictyum*” = 51.25%.

Assemblage	Species	Contribution %	Cumulative contribution %
<i>Thena muricata</i>	<i>T. muricata</i>	100	100
Axinellids	<i>A. damicornis</i>	85.55	85.55
	<i>A. verrucosa</i>	9.62	95.18
<i>Haliclona mediterranea</i>	<i>H. mediterranea</i>	82.74	82.74
	<i>Siphonochalina</i> sp. 2	10.08	92.83
	<i>T. aurantium</i>	3.28	96.1
“Haliclonid-Aplysina”	<i>H. cf. elegans</i>	52.53	52.53
	<i>H. mediterranea</i>	10.84	63.37
	<i>A. cavernicola</i>	5.72	69.1
	<i>A. damicornis</i>	4.66	73.76
	<i>A. cf. pseudominuta</i>	4.2	77.95
	<i>H. implexa</i>	4.06	82.02
	<i>Haliclona</i> sp. 1	3.41	85.43
	<i>Haliclona</i> sp. 10	2.76	88.19
	<i>Rhabderemia</i> sp.	1.88	90.07
	<i>H. poecillastris</i>	1.76	91.83
	<i>H. fulva</i>	1.72	93.55
	<i>Hamacantha</i> sp.	1.71	96.25
“ <i>Rhabderemia-Diclyonella</i> ”	<i>Rhabderemia</i> sp.	51.26	51.26
	<i>Diclyonella</i> sp. 1	28.02	79.28
	<i>H. falcu</i>	5.58	84.86
	<i>P. compressa</i>	5.53	90.39
	<i>H. cf. dedritifera</i>	5.27	95.65
“ <i>Hamacantha-Tretodictyum</i> ”	<i>H. falcu</i>	76.61	76.61
	<i>T. reisi</i>	10.30	86.91
	<i>H. mucosa</i>	6.64	93.84
	<i>H. cf. dedritifera</i>	2.84	96.68

3.2. Relationship with environmental parameters

The environmental variables used in our analysis explained ~34.4% of the total inertia in the CCA, with the first two axes accumulating 15.86% of the variance. Named based on their dominant contributing species (Fig. 4b), six sponge assemblages (identical to those identified by the cluster analysis) were differentiated in the CCA (Fig. 4a), which shows the relations of their presence to the examined environmental factors (Fig. 4c). Depth strongly segregates the Menorca Channel sponge assemblages into those occurring on the continental shelf, the shelf break and the upper slope. On horizontal rocky bottoms of the inner continental shelf the sponge fauna was

characterized by *A. damicornis* and *A. verrucosa* (the Axinellid assemblage; Fig. 5; Supplementary material 3). Horizontal maërl beds of the inner continental shelf were mainly characterized by the *Haliclona mediterranea* assemblage (Fig. 6; Supplementary material 4). On horizontal maërl beds, cobble grounds and rocky substrates of the outer continental shelf the sponge fauna was characterized by *Haliclona* species (mainly *H. cf. elegans*, *H. implexa*, *Haliclona* sp. 1), *A. cavernicola* and *Hamacantha* sp. (the “Haliclonid-Aplysina” assemblage; Fig. 7; Supplementary material 5). On sandy grounds of the shelf break *T. muricata* was the only sponge species (the *Thena muricata* assemblage; Fig. 8a). *Rhabderemia* sp. and *Diclyonella* sp. 1 dominated sloping rocky grounds of the shelf break, along with the fan-shaped sponge *Poecillastra compressa* (the “*Rhabderemia-Diclyonella*” assemblage; Fig. 8b-g; Supplementary material 6). Finally, sloping and vertical rocky substrates of the upper slope were dominated by *H. falcu* and *T. reisi* (the “*Hamacantha-Tretodictyum*” assemblage; Fig. 8h-i; Supplementary material 7).

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.dsr.2017.11.003>.

3.3. Variation of sponge diversity with depth

Beta-diversity of sponges decreased with depth, being considerably higher on the continental shelf compared to the shelf break and slope (Fig. 9). Both species richness and the exponent of Shannon's Index (Fig. 10) presented peaks at 70–90 m depth (Fig. 10). We observed an acute plummeting of species numbers and the exponent of Shannon's index at the beginning shelf break (~110–130 m depth). Below that, a small increase in species richness, and an evenness-diversity peak occurred at the transition between the shelf break and the upper slope (170–190 m depth). Finally, that was followed by gradual decreases in these measures down to 250–270 m depth, where both species richness and diversity were lowest. Diversity values remained more or less stable on the remaining upper slope.

4. Discussion

4.1. Representative size of the sampling unit

The area selected to determine sponge assemblages in our study (20 m²) considerably exceeds that of other work performed in neritic environments (Weinberg, 1978; Coppari et al., 2016). In coastal areas, environmental features change dramatically at very small scales (Garrabou et al., 2002), so that small sample areas can include large parts of the regional faunal diversity. Conversely, environmental conditions on continental shelves and slopes worldwide generally remain constant over vast areas (Snelgrove and Smith, 2002). In these deeper environments, small-scale (e.g. random disturbances; Rex, 1981) and regional-scale processes (e.g. barriers and re-colonization;

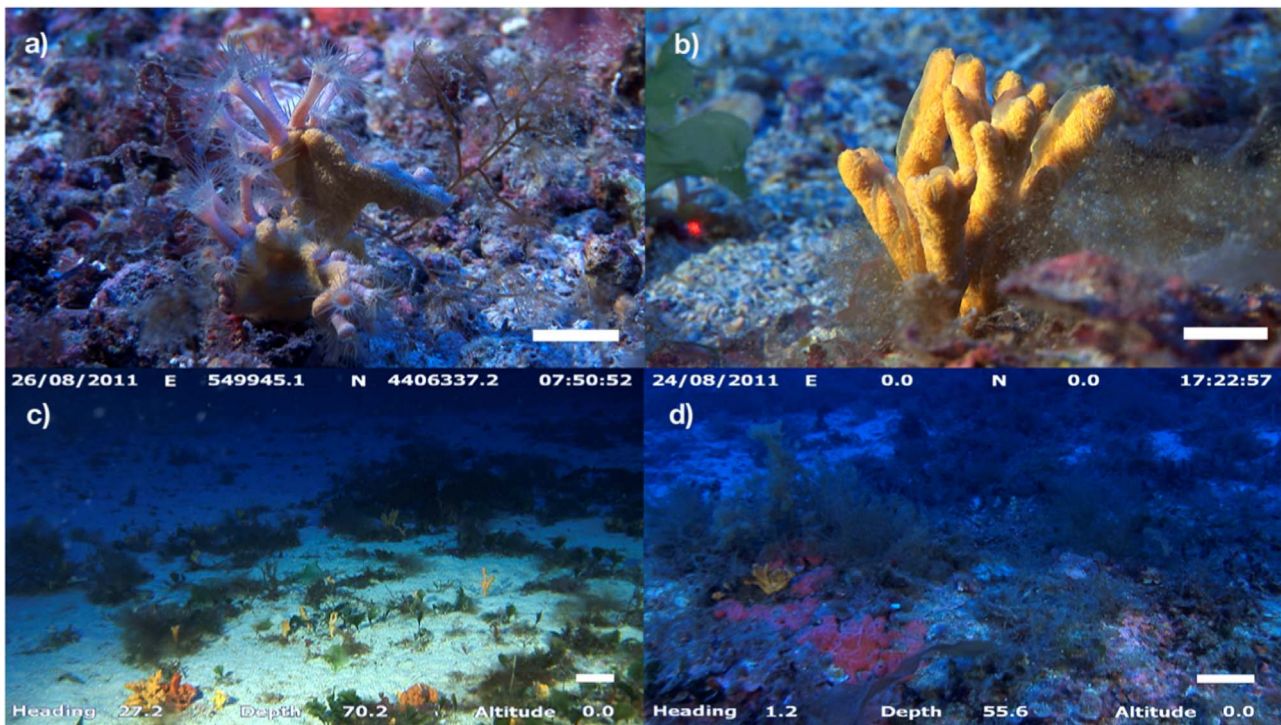


Fig. 5. Axinellid assemblage. (a) Close up of *Axinella damicornis* in association with *Parazoanthus axinellae*, (b) close up of *Axinella verrucosa*, (c) *A. damicornis* and *A. verrucosa* facies atop of a partially sand-covered rock, (d) *A. damicornis* individuals observed under a dense algal canopy, with *Crambe crambe* growing on the exposed areas of the rocky bottom. Scale bar: 1 cm (a, b) and 10 cm (c, d).

only occurred on horizontal maërl beds. It was mainly dominated by *Haliclona (Reniera) mediterranea*, a well-known inhabitant of Mediterranean coralligenous communities (Griessinger, 1971; Ballesteros, 2006; Bertolino et al., 2013). Species belonging to this assemblage have also been found in maërl beds, but rather sparsely, on the Tunisian shelf, at depths of 50–60 m where trawling takes place (El Lakhrach et al., 2012). This pattern contrasts with that observed in our study area, where *H. mediterranea* occupied vast areas of the inner continental shelf. No other records can be found in the literature that restrict this assemblage to maërl beds, despite the prevalence and wide distribution of its dominant species along the northwestern edges of the Mediterranean basin (Griessinger, 1971).

Around 70 m depth, we observed that the Axinellid, *Haliclona mediterranea* and “Haliclonid-Aplysina” assemblages occasionally overlapped. It is common for assemblages to change gradually from one to another across a variable transition zone (ecotone), where the numbers of species often increase due to assemblage overlap (Bellan-Santini, 1985). In this transition zone, *H. cf. elegans* and *H. mediterranea* were the dominant species, co-occurring with *A. damicornis* and *A. verrucosa*, where the highly sciaphilous *A. cavernicola* (Maldonado and Uriz, 1995) was completely absent. So, this zone appears to be the transition depth (70 m) between the inner (Axinellid and *Haliclona mediterranea*

assemblages) and outer (“Haliclonid-Aplysina”) shelf assemblages, the shift most likely being triggered by changing light penetration (Ballesteros, 2006).

From the outer continental shelf down to the upper limit of the shelf break (~70–110 m depth) the “Haliclonid-Aplysina” assemblage occurs on horizontal maërl beds as well as on vertical rocks. This agrees with previous studies in the Mediterranean Sea, where *Aplysina cavernicola* and *Haliclona cf. elegans* have been observed inhabiting both horizontal maërl (Griessinger, 1971; Maldonado and Uriz, 1995) and vertical coralligenous substrates (Uriz et al., 1992; Cocito et al., 2002). As described by Vacelet (1969) for offshore rocky-bottom (*roche du large*) communities, we observed two distinctive morphologies of *Haliclona poecillastroides*: (1) laminar, in close contact with the substrate, mostly present on sloping or vertical surfaces, and (2) fan-shaped, present almost exclusively on horizontal surfaces (Fig. 8c).

Ballesteros (1991) and Augier and Boudouresque (1975) defined two well-differentiated algal communities, the *Lythophyllo-Halimedetum tunae* and the *Rodriguezelletum-straforellii*, occurring on maërl and coralligenous substrates. We reported the co-occurrence of the Axinellid and *Haliclona mediterranea* assemblages and the *Lythophyllo-Halimedetum tunae* algal community and, to a lesser extent, co-occurrence of the “Haliclonid-Aplysina” and *Rodriguezelletum-straforellii* groupings.

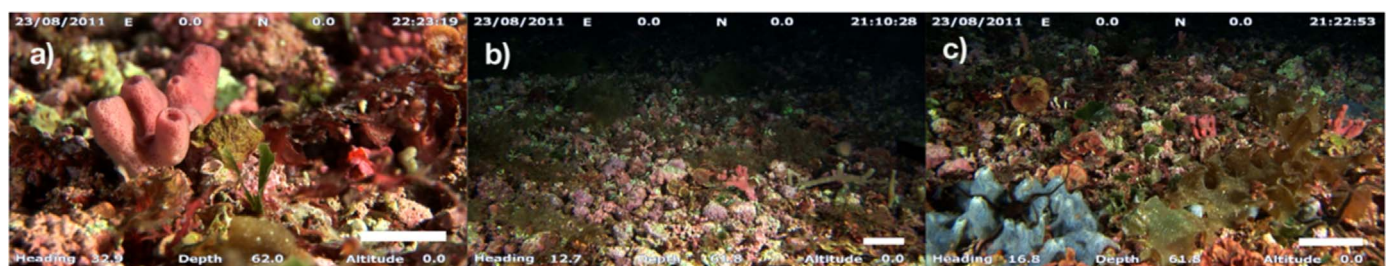


Fig. 6. *Haliclona mediterranea* assemblage. (a) Close up of *Haliclona (Reniera) mediterranea*, (b) *H. mediterranea* and *Siphonochalina* sp. 2 growing on maërl beds within a facies of *Flabellia* spp., (c) A close up of *Phorbas tenacior* individual growing next to *H. mediterranea*. *Peyssonnelia* spp. and *Flabellia* spp. algae can be seen. Scale bar: 10 cm.

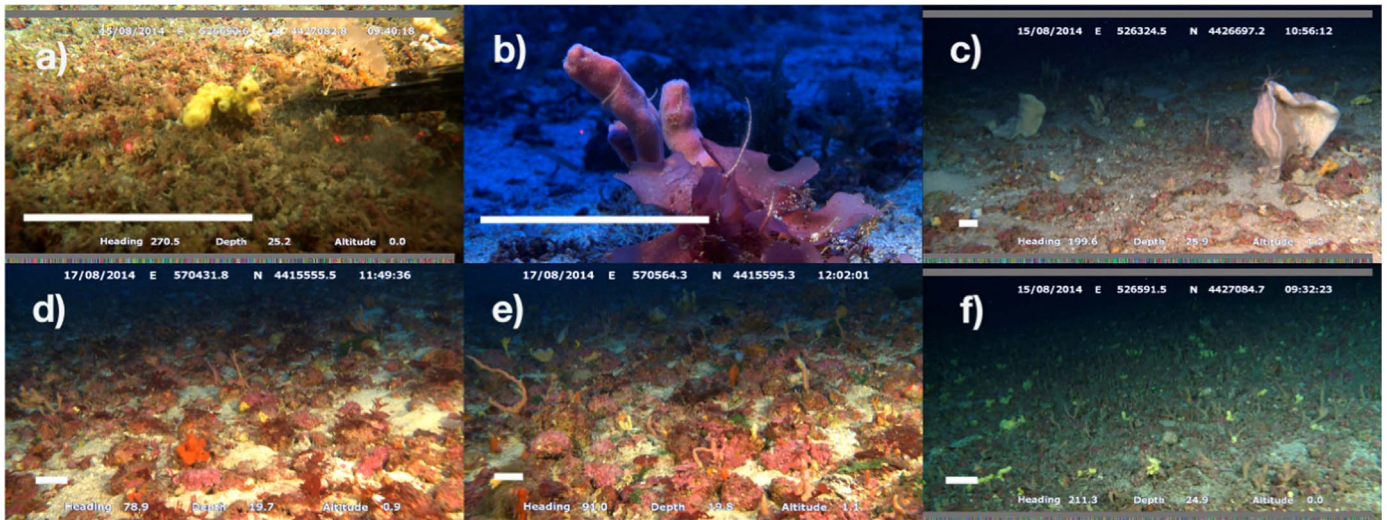


Fig. 7. “Haliclonid-Aplysina” assemblage. (a) Close up of *Aplysina cavernicola*, (b) Close up of *Haliclona cf. elegans* growing among laminar red algae (“mixing area”), (c) Overview of “Haliclonid-Aplysina” at outer areas of the continental shelf, with *H. cf. elegans* and the fan-shaped *Haliclona poecillastroides*, (d, e) View of the transition zone (70 m depth; upper limit of the “Haliclonid-Aplysina”), with *H. cf. elegans*, *H. mediterranea*, *Axinella damicornis* and the orange-encrusting *Haliclona (Halichoclona) fulva*. Red laminar algae and the green-encrusting *Palmophyllum crassum* dominate the algal community (f) view of the *A. cavernicola* (yellow) *H. cf. elegans* (pink) growing atop of maërl beds at the lower distribution of the assemblage. Scale bars 4 cm (a, b) and 10 cm (c-f).

We thus propose that the sponge assemblages and algal communities are associated in the area and are probably limited by the same driving factor: the gradient in irradiance penetration (Uriz et al., 1992; Ballesteros, 2006).

At the shelf break (~110–180 m depth) sponge assemblages were clearly segregated by substrate type. Sandy-muddy bottoms were home to the *Thenea muricata* assemblage, with only *Thenea muricata* individuals present. *T. muricata* is a fairly common species on similar

bottoms around the Mediterranean Sea (Pansini and Musso, 1991), ranging from ~50 m depth to the abyssal plain (Uriz and Rossell, 1990). It is known to be susceptible to bottom trawling (Pansini and Musso, 1991) and is a common species in the trawling by-catch in the Menorca Channel (Massutí and Reñones, 2005). Thus, trawling, combined with the limited availability of suitable soft bottoms (Grinyó, 2016) could explain its narrow distribution in our study area.

The “*Rhabderemia-Dictyonella*” assemblage mainly occurred on

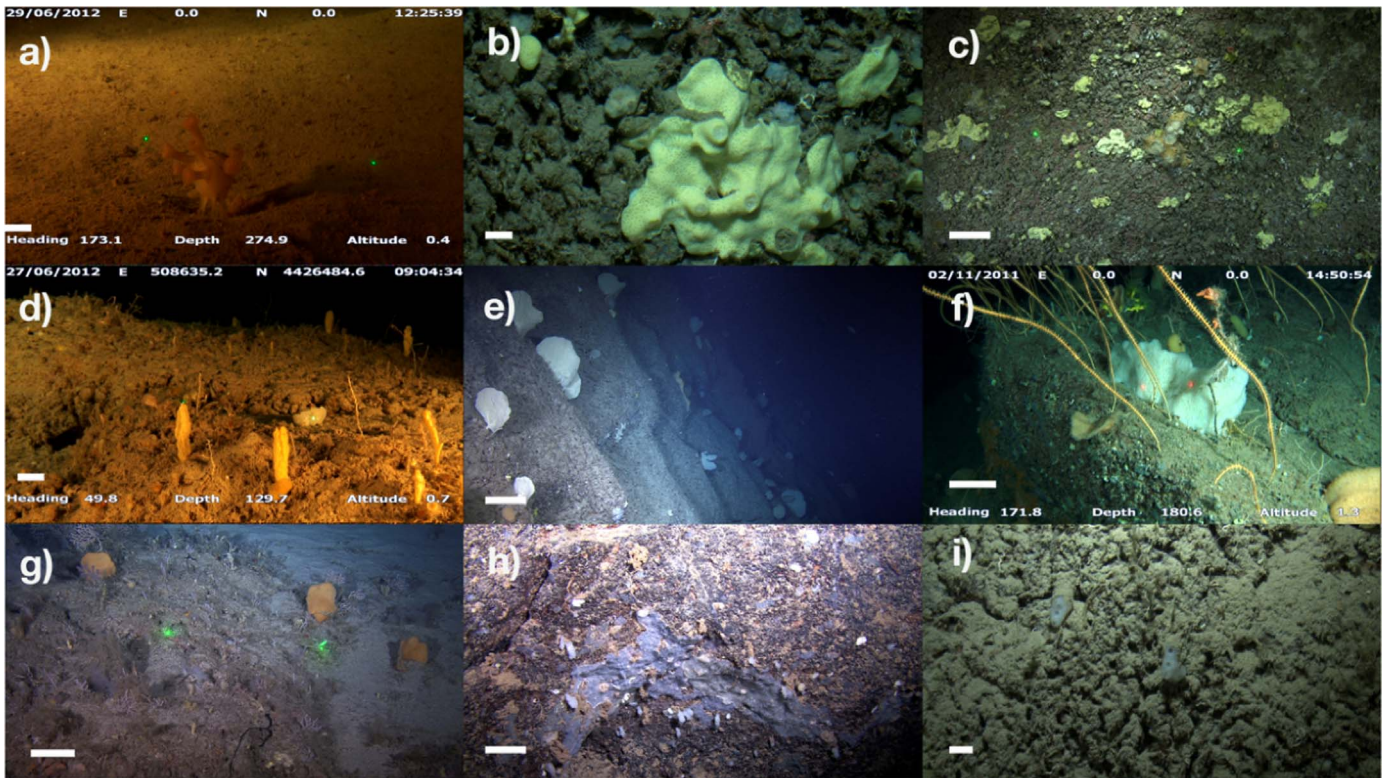


Fig. 8. *Thenea muricata* assemblage. (a) Close up of *Thenea muricata*; “*Rhabderemia-Dictyonella*” assemblage (b) Close up of *Rhabderemia* sp., (c) *Rhabderemia* sp. facies on a vertical wall, (d) Facies of *Dictyonella* sp. 1 on a horizontal rocky surface, (e) Facies of the fan-shaped sponge *Phakellia robusta* growing on a vertical wall, (f) *Pachastrella monilifera* (white) and *Poecillastra compressa* next to a facies of the gorgonian *Viminella flagellum*, (g) *Poecillastra compressa* individuals; “*Hamacantha-Tretodictyum*” assemblage, (h) *Hamacantha (Vomerula) falcata* (grey-blue) and several *Tretodictyum reisiwi* individuals growing on a vertical wall, (i) Close up of *T. reisiwi* individuals. Scale bar 1 cm (a, b, i) and 10 cm (c-h).

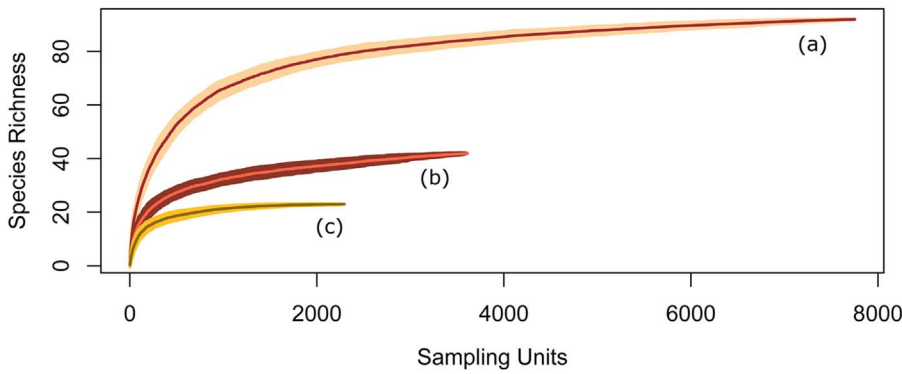


Fig. 9. Randomized species accumulation curves calculated for each depth range. (a) Continental shelf (50–110 m depth); (b) shelf break (110–180 m depth); (c) upper slope (180–350 m depth). Coloured areas along each line represent a 95% confidence interval for each bathymetric range.

rocky substrates at the shelf break (110–180 m depth) and on the upper slope (180–350 m depth). *Rhabderemia* sp. and *Dictyonella* sp. 1 dominated this assemblage, following the distribution pattern described by Vacelet (1969). Vertical and sloping rocky bottoms in this zone were inhabited primarily by encrusting sponges (*Rhabdaremia* sp.), whereas columnar sponges (*Dictyonella* sp. 1) were more characteristic of horizontal rocky bottoms. Fan-shaped sponges (> 20 cm width), such as *Poecillastra compressa*, and, to a lesser extent, *Phakellia robusta*, *Pachastrella monilifera* and *Phakellia hironellei* were also present in this assemblage.

Bo et al. (2012) have highlighted the paramount roles of large, fan-shaped sponges in providing habitat, shelter and food to a wide range of

associated, vagile fauna. However, in our results, the “*Rhabderemia-Dictyonella*” assemblage was dominated by encrusting sponges (~63%), with fan-shaped (~6%) and erect species (~28%) being considerably less abundant. This is in contrast with the results of Bo et al. (2012) who reported fan-shaped species dominating over encrusting ones in the Bari Canyon (Southern Adriatic Sea). Such differences could be explained by the much higher sedimentation rates reported in the Bari Canyon (Turchetto et al., 2007) compared to the Balearic Archipelago (Pasqual et al., 2015; Grinyó et al., 2017), as higher sediment accumulation can limit the presence of encrusting sponges that can become smothered.

Finally, the “*Hamacantha-Tretodictyum*” assemblage occurred on

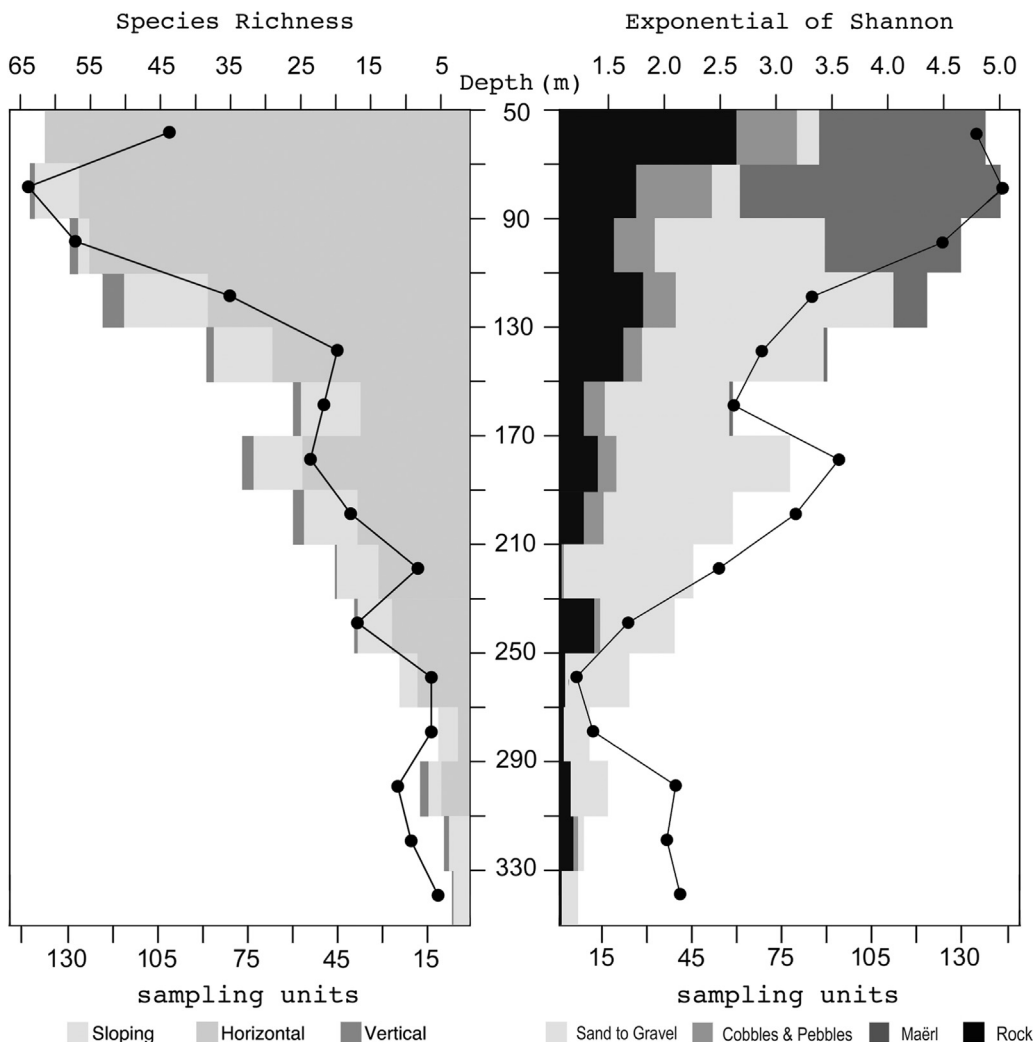


Fig. 10. Distribution with depth of species richness and the exponential of Shannon's index. Depth is divided into 20 m intervals, with the number of species and diversity represented as black dots. Black-to-grey scale histograms represent the total numbers of sampling units for each substrate type and degree of slope (see legend) over the studied bathymetric range.

rocky walls on the upper slope at ~230–350 m depth. It consisted mostly of the encrusting sponge *Hamacantha (Vomerula) falcula* and the hexactinellid *Tretodictyum reisiwigi*, both known to be frequent on the upper slope (below 400 m depth) along the French (Pedel and Fabri, 2011; Fourt et al., 2017) and Italian (Taviani et al., 2017) Mediterranean coasts. Moreover, *T. reisiwigi* has only been known previously in the Balearic archipelago from the Emile Baudot seamount (Maldonado et al., 2015). Its presence in the Channel is a new addition to the known Menorca sponge fauna and supports the view that *T. reisiwigi* is very likely widespread around the Mediterranean basin (Bourny-Esnault et al., 2017).

4.3. Depth-diversity distribution

Diversity of megabenthic sponge species in the Menorca Channel was higher than that reported for other Mediterranean littoral and neritic areas (Bibiloni, 1990; Maldonado and Uriz, 1995; Cocito et al., 2002; El Lakhrech et al., 2012). More than 100 large sponge species were observed between 50 and 350 m depth, which is a high diversity in agreement with previous records from the Balearic Sea (Bibiloni, 1990). The sponge assemblages observed in the Menorca Channel followed the bathymetric pattern commonly described for other areas: Demospongiae contributed the dominant species over the entire range, from 50 to 350 m depth, whereas calcareous and homoscleromorph sponges were restricted to the inner continental shelf (Van Soest et al., 2012) and hexactinellid sponges appeared at around 200 m depth (Reid, 1968).

Highest diversity values were concentrated on the outer continental shelf (70–110 m depth), followed by an abrupt decline that continued progressively downward. This pattern may be a response to several, interacting environmental factors: light intensity, substrate type, habitat heterogeneity, other competing organisms and hydrodynamic patterns. Highly illuminated shallow environments tend to be dominated by algae, which may exclude the presence of sessile organisms with slower growth rates (Maldonado and Young, 1996; Witman and Dayton, 2001). This phenomenon, termed “depth emergence”, is the increase of macroinvertebrate abundance and diversity with depth, coinciding with the disappearance of the algal turf (Witman and Dayton, 2001). Thus, the initial increase we observed in species richness and diversity (from 50 to 90 m depth) could be driven by the decreased light intensity, favoring the presence of a more diverse invertebrate fauna (Kefalas et al., 2003). The presence of well-developed coralligenous outcrops and maërl beds, characterized by the more diverse “Haliclonid-*Aplysina*” assemblage (> 50 species), also enhances sponge diversity close to the shelf break. In addition, cryptic species could potentially increase the observed diversity values, if they could be successfully determined and identified (Bertolino et al., 2013). Ocean currents and tides have also been suggested to favor the development of dense aggregations of benthic suspension feeders on the shelf break, as the area provides an abundant and stable food supply to them (Thiem et al., 2006). Finally, the merging of continental shelf and slope faunas on the shelf break may play a role in establishing the high shelf-break diversity, a sort of mid-domain effect (Colwell and Lees, 2000). However, the abrupt decline in sponge diversity occurring just below the shelf break, which is also observed in other areas (e.g., the Bahamian Slope, Maldonado and Young, 1996), could derive from the disappearance of coralligenous outcrops and maërl beds, coupled with a marked overall decrease in the heterogeneity of substrates. At the Menorca Channel's shelf break and upper slope, soft sediments dominated over hard substrates. Sponge diversity at the shelf break and upper slope is strongly linked to the presence of hard and vertical substrates, where encrusting sponges dominate the community (Maldonado and Young, 1996). On the contrary, deep soft sediments harbor very low sponge diversity around the Mediterranean Sea (Fourt et al., 2017). This could explain the observed diversity pattern and also

explain the diversity peak at 170–190 m that coincided with the presence of vertical walls.

5. Conclusions

More than 40,000 sponges individuals belonging to 109 taxa were observed to inhabit the deep areas of the Menorca Channel area. This high number of species reflects the interactions among multiple environmental factors, which creates a variety of niches and favors development of multiple sponge assemblages. Overall, six different assemblages were identified inhabiting distinctive shelf and slope environments, with depth and substrate type being the important factors establishing these species associations. The high densities of particular species in many locations indicate that a pool of millions of individuals inhabits the whole study area. Thus, we believe that the Menorca Channel harbors one of the best-conserved, best-developed sponge assemblages recorded and remaining to date in the Western Mediterranean. Due to the imminent establishment of this area as a marine protected area (MPA), it is of paramount importance to increase our knowledge about the distributions, population size structures and vulnerabilities to anthropogenic stressors of its most representative species. We need a quantified and objective faunal baseline to support implementation of effective management and monitoring measures. The present study is a contribution towards meeting that goal.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr.2017.11.003>.

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