Progress in Oceanography 162 (2018) 40–51

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

Megabenthic assemblages in the continental shelf edge and upper slope of the Menorca Channel, Western Mediterranean Sea

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ARTICLE INFO

Keywords:
Mediterranean Sea
Continental shelf edge
Continental slope
Benthic communities
Trawling
Spatial and vertical distribution

ABSTRACT

Highly diverse megabenthic assemblages dominated by passive and active suspension feeders have been recently reported in shelf edge environments of the Mediterranean Sea. Due to their frequent association with species of commercial interest, these assemblages have been heavily impacted by fishing. The vulnerability and low resilience of these assemblages, composed mainly by long-living and slow-growing species, have motivated the implementation of management measures such as the restriction of bottom trawling, and the establishment of large protected areas embracing these environments. The Menorca Channel is one of such areas recently included in the European Union Natura 2000 network. Quantitative analysis of video transects recorded at 95–360 m depth by manned submersible and remotely operated vehicles were used to characterize megabenthic assemblages and to assess their geographical and bathymetric distribution. Six different assemblages were identified, mainly segregated by substrate type and depth. Hard substrates hosted coral gardens and sponge grounds, whereas soft sediments were mainly characterized by large extensions of the crinoid *Leptometra phalangium* and the brachiopod *Gryphus vitreus*. The good preservation of most of the observed assemblages is probably related to a low bottom trawling pressure, which mainly concentrates deeper on the adjacent continental slope. Because of their biological and ecological value, management and conservation measures need to be established to preserve these benthic assemblages.

1. Introduction

Recent technological advances and increased availability of remotely operated vehicles (ROVs), manned submersibles, and video-equipped towed gears have significantly increased accessibility to mid and outer continental shelves, continental slopes, submarine canyons and seamounts, thus allowing the direct observation and quantitative study of megabenthic assemblages (e.g. Etiope et al., 2010; Buhl-Mortensen et al., 2017; Pierdomenico et al., 2016). Rich and highly diverse megabenthic assemblages mostly dominated by passive (e.g. gorgonians, corals and black corals) and active (e.g. sponges) suspension feeders, have been recently reported on these environments in several locations of the Mediterranean Sea (Emig, 1997; Bo et al., 2009, 2012, 2013, 2015; Deidun et al., 2014; Bertolino et al., 2015). These assemblages provide habitat (Mastrototaro et al., 2010; Porteiro et al., 2013) and act as nurseries (Colloca et al., 2004; Bo et al., 2015) for a wide variety of associated species, many of which are of commercial interest (Abella et al., 2005; Maynou and Cartes, 2012).

These assemblages have been largely exposed to long-line and trammel net fishing (Orejas et al., 2009; Sampaio et al., 2012; Mytilineou et al., 2014) as well as to the impacts of bottom trawling, since they are distributed below 50 m depth where bottom trawling is allowed (Council Regulation (EC) No 1967/2006) (Maynou and Cartes, 2012; Fabri et al., 2014). Such fishing practices have dramatic effects on megabenthic structural species, which are often removed or severely damaged (Fosså et al., 2002; Mytilineou et al., 2014), resulting in a decline in the biodiversity and abundance of the associated fauna (Althaus et al., 2009; Clark et al., 2016). In the Mediterranean Sea, bottom trawling has progressively increased in intensity since the first half of the 20th century and has steadily expanded toward greater

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https://doi.org/10.1016/j.pocean.2018.02.002
Received 5 November 2016; Received in revised form 8 January 2018; Accepted 6 February 2018

depths (Sacchi, 2008). Consequently, decades of chronic trawling have widely impacted large areas of the Mediterranean continental shelf and slope (e.g. Fabri et al., 2014), limiting relatively well preserved megabenthic assemblages to remote (Díaz et al., 2015) or inaccessible rough, rocky floors (Bo et al., 2015). The ecological effects of bottom trawling are extremely long lasting, since the recovery of deep megabenthic assemblages dominated by anthozoans is limited (Bennecke and Metaxas, 2017) or absent (Althaus et al., 2009; Williams et al., 2010) in areas closed to trawling for more than ten years. Due to the slow-growth and high longevity of most of the megabenthic species in these assemblages, it has been suggested that their possible recovery could span from centuries to millennia (Clark et al., 2016).

The vulnerability and low resilience of these communities (Althaus et al., 2009) have motivated the recent establishment of managed or protected areas on continental shelves, continental slopes (Spalding et al., 2013; Bennecke and Metaxas, 2017), submarine canyons (Marin and Aguilar, 2012) and seamounts (Sheppard et al., 2012; Huvenne et al., 2016) worldwide. In the Mediterranean Sea, the protection of large areas of the continental shelf and slope has been recently proposed as a part of an ecosystem-based management strategy of marine resources and environments, which include the Menorca Channel (European Union, Natura 2000 network, http://www.eea.europa.eu/data-and-maps/data/natura-2). Previous studies have investigated and characterized benthic assemblages in the inner continental shelf (< 100 m) of the Menorca Channel (e.g. Joher et al., 2012; Barberá et al., 2012; Grinyó et al., 2016), but the composition and distribution of benthic assemblages on the outer continental shelf and upper slope still remain widely unknown. Additional information is thus fundamental for the establishment of effective management and conservation measures, as well as to monitor their effectiveness.

Hence, the aims of this study were: (1) to characterize the composition of megabenthic assemblages (defined here as assemblages constituted by sessile and low motile invertebrates (i.e. echinoderms) larger than 2 cm (e.g. Seike et al., 2013)) on the outer continental shelf and upper slope at 95–360 m depth in the Menorca Channel; (2) to assess their geographical and bathymetric distribution; (3) to quantify how biodiversity changes with depth; and (4) to compare their distribution with the pressure of bottom trawling in the area.

2. Materials and methods

2.1. Study area

The Menorca Channel is located in the Western Mediterranean Sea between Mallorca and Menorca islands (Fig. 1a), as part of the Balearic Promontory (Acosta et al., 2002). The study area includes the outermost continental shelf (90–110 m), the shelf edge (110–180 m) and the upper slope (180–350 m) of the channel. The continental shelf is characterized by smooth reliefs, covered by maërl beds alternating with outcropping rocks covered by coralligenous concretions, and detritic coarse sediments (Barberá et al., 2012). Fine sands cover vast areas of the northern part of the investigated sector of the continental shelf at 100–110 m depth (Grinyó et al., 2016). Smooth reliefs and large extensions of detritic sediments with few isolated patches of outcropping rocks characterize most of the shelf edge and continental slope (Grinyó et al., 2016). Vertical walls and sharp-edged rocky outcrops are the dominant substrate near Cap Formentor (Fig. 1b) and in the Menorca Canyon head (Fig. 1c) (Grinyó et al., 2016).

The northern shelf edge and continental slope of the Menorca Channel are influenced by the Balearic Current (Balbín et al., 2012), which flows northward at approximately 200 m depth (Ruiz et al., 2009). Conversely, the southern shelf edge and upper slope are mostly influenced by the sporadic arrival of mesoscale structures detached from the Algerian Current and the Almería Oran front (Millot, 1987; García et al., 2005).

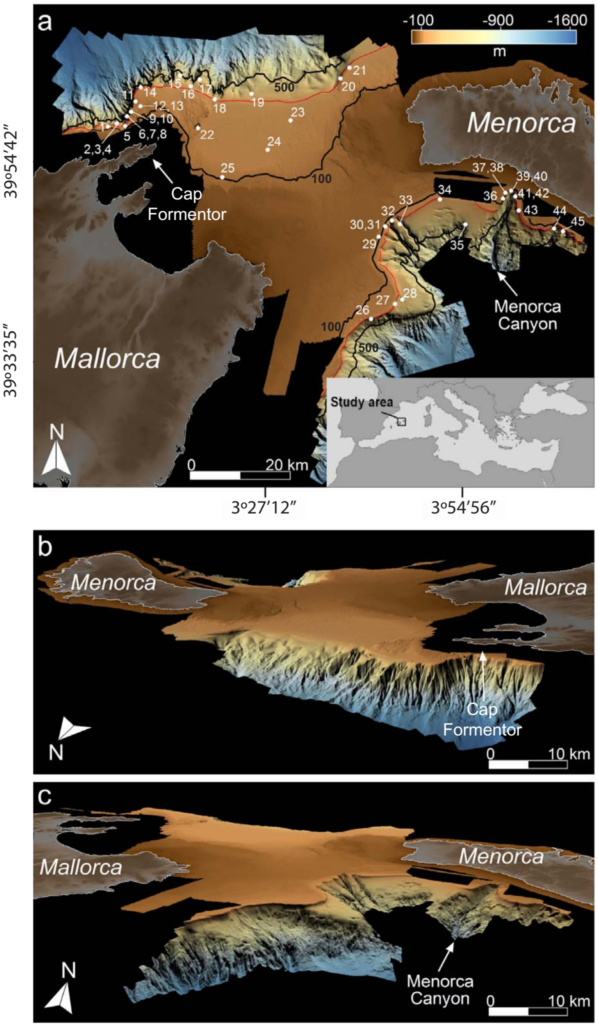

Fig. 1. The study area. (a) Bathymetry of the Menorca Channel: the map shows the location of the video transects (1–45) and the location of the study area in the western Mediterranean (inset at the bottom right). Frontal views of the continental slope of the north (b) and south (c) of the Menorca Channel with the continental shelf in the background. Black lines indicate the 100 and 500 m isobath and the red line indicates the shelf edge. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Sampling procedure

A total of 45 video transects (Fig. 1a, Supplementary material 1) were recorded during four surveys conducted on board R/V “García del Cid” (September 2010, April 2011, October 2011, June 2012): 17 video transects were recorded with the manned submersible JAGO (IFM–GEOMAR) during the first two surveys, and 28 video transects were recorded with the NEMO ROV (Gavin Newman) during the last two surveys. Instruments were equipped with a high definition camera (1080 × 1920 resolution), a manipulator arm and two parallel laser beams (0.5 m and 0.12 m for the JAGO and the NEMO, respectively). Laser beams were used to determine a fixed width of 0.5 m during video analysis and all transects were recorded with a close zoom (~ 0.5–1.5 m width). Both JAGO and NEMO moved at a constant speed of ~ 0.3 knots, and explored a depth range between 90 and 347 m. The positioning of JAGO and NEMO was achieved with an underwater acoustic positioning system LinkQuest TrackLink 1500 HA. Transects were haphazardly located in order to cover the entire study area, but areas showing morphological features possibly related to the presence of rocky bottoms were explored more intensively (Fig. 1). Overall, a total seabed length of 37.7 km was video recorded.

In order to confirm the taxonomic identification of the megabenthic organisms observed in the video transects, organisms of all 69 species considered in this study were collected by means of the JAGO and the NEMO manipulator arm, and epibenthic sledges equipped with video cameras. Sampled organisms were fixed and preserved in 10% formalin as well as in absolute ethanol for posterior taxonomical and genetic analyses, respectively. Organisms were identified taxonomically to the lowest possible level.

2.3. Video analysis

Quantitative video analysis was performed according to the methodology described by Gori et al. (2011) and Grinyó et al. (2016), using Apple's Final Cut Pro software. The length of each transect was estimated based on the records from the acoustic positioning system (see details in Grinyó et al., 2016). Sequences with poor image quality or too far away from the seafloor were considered unsuitable for analysis. The remaining useful sequences comprised 93.3% of the total recorded material and corresponded to a total distance of 35 km. The position of all megabenthic organisms observed within a width of 0.5 m (estimated video coverage based on the laser beams) was defined by the time elapsed since the beginning of the video transect to the crossing of the laser beams by the organism (see details in Grinyó et al., 2016). Seabed substrate type was classified (based on the Wentworth scale and previous studies in the Menorca Channel (Santín et al., 2018)) into five categories: fine sand, medium sand to gravel, cobbles and pebbles, maërl, and rock. Seabed slope was classified into three categories: horizontal (0–30°), sloping (30–80°), or vertical (80–90°); slope was estimated from the video by looking at the depth sensor (Gori et al., 2011; Ambroso et al., 2013; Grinyó et al., 2016).

2.4. Data treatment

2.4.1. Sampling unit characterization

Each transect was divided into fragments of equal distances, hereafter designated as sampling units. Several sampling unit sizes (2, 5, 10, 15, 20, 30, 40 and 50 m^2) were used in the canonical correspondence analysis (see below) in order to explore how sampling unit size may affect the identification of the benthic assemblages, and their associated main environmental features. Each sampling unit was characterized by the number of megabenthic organisms of each identified species (density = number of individuals per m^2), as well as by the average depth and coverage percentage for each substrate and slope category.

2.4.2. Canonical correspondence analysis

Canonical correspondence analysis (CCA) is a multivariate constrained ordination technique used to elucidate the relationships between species abundances (response variables) and environmental variables (explanatory variables) (Ter Braak, 1986; Greenacre and Primiceiro, 2013). CCA was used to define megabenthic assemblages based on species composition, and to explore their relationship with the three environmental factors obtained from the video transects: substrate, depth, and slope. Since recording of video transects was restricted in time, other environmental variables such as seawater temperature, turbidity or fluorescence were not considered. Taxa that appeared with less than three individuals were discarded from the analysis in order to avoid distortions that could be produced by rare data. Depth of sampling units was coded into four fuzzy categories that preserve all the information in the variables while reducing it to a categorical scale (Aschan et al., 2013). Such fuzzy-coding takes into account possible nonlinear relationships between fauna abundance and depth (Greenacre and Primiceiro, 2013). The mean depth of each of the four fuzzy categories are as follow: dep1 = 106 m, dep2 = 130 m, dep3 = 188 m, and dep4 = 252 m. No transformation was applied to either environmental or biological data. The CCA was performed with the function cca in the "vegan" package (Oksanen et al., 2015) of the R software platform "R Core Team 2014". Additionally, substrate, depth, and slope were tested to determine which was the best predictor by means of the R function anova in the "vegan" package (Oksanen et al., 2015). Due to the lack of previous information about sampling unit size for the characterization of Mediterranean megabenthic assemblages in the outer continental shelf and upper slope by means of quantitative video analysis, CCA was performed with different sampling unit sizes (2, 5, 10, 15, 20, 30, 40 and 50 m^2).

2.4.3. Megabenthic assemblages distribution and depth-related diversity

The geographical distribution of each identified megabenthic assemblage in the study area was reported by mapping its occurrence in the video transects on a geographically referenced map using GIS (ESRI ArcGIS ArcInfo v10). The bathymetric distribution of each assemblage was represented in 5 m depth intervals.

To compare species' turnover (or beta-diversity) amongst the outer continental shelf (90–110 m depth), the shelf edge (110–180 m depth) and the upper slope (180–347 m depth) randomized species accumulation curves were calculated (Vetter et al., 2010; De Leo et al., 2014), using the statistical software R and the "vegan" package.

The method used finds the mean species accumulation curves and their standard deviation from random permutations of data (n = 100), which avoids distortions in the curves due to variations in species abundance and sampling effort (Gotelli and Colwell, 2001).

2.4.4. Fishing activity in the study area

Fishing activity and location of fishing grounds (i.e. areas consistently fished through time) in the study area were assessed by means of Vessel Monitoring System (VMS) location data through the analysis of the number of fishing events per surface units. VMS data were obtained in the framework of the LIFE + INDEMARES project from the General Directorate of Fisheries Management of the Spanish Ministry of Agriculture, Food and Environment (MAGRAMA). Available VMS records from January 2007 to July 2012 were included after examination to exclude erroneous vessel identity, position or speed. To select the records referring to fishing activity, a set of common criteria (Lee et al., 2010) was followed: duplicated records and records close to ports were removed, and the interval between records was calculated in order to only retain vessels moving at 2–3.5 knots, so that only vessel locations while trawling are considered. The distribution of fishing activity in the study area was assessed based on fishing events counts per cell unit based on a point summation method (Hintzen et al., 2010). A 250 m^2 cell was selected as the most suitable size considering geographical factors and the available dataset (for further details, see Piet and Quirijns, 2009). Only one record per vessel, day and cell was retained to avoid overestimation of fishing activity (Hintzen et al., 2010). The centroids of each cell were extracted and weighted by the sum of fishing events for this cell. These weighted centroids were used to identify statistically significant hot spots of fishing activity in the study area using the Gi^* statistic (Getis and Ord, 1996).

3. Results

A total of 69 megabenthic species belonging to seven phyla and twelve classes were identified in the study area (Supplementary material 3).

3.1. Canonical correspondence analysis (CCA)

CCA analysis performed with different sampling unit sizes revealed a general increase in the amount of inertia explained (i.e. explained variation of the data) by environmental factors as sampling unit size increased (Table 1). However, as sampling unit size increased, the resolution of the CCA output decreased (Table 1, Supplementary material 2). This was due to: (1) a reduction in the total number of sampling units, (2) an increase in the number of sampling units discarded from

Table 1
Results of the CCA analysis performed at different sampling unit size (env. fact. = environmental factors).

Sampling unit size (m^2)	Species number	Organism number	Sampling units number	Total inertia	Restricted inertia	Unrestricted inertia	% of inertia explained by env. fact.	Megabenthic assemblage number
2	69	39,138	8639	28.36	3.03	25.32	10.69	6
5	69	38,230	3372	20.96	3.28	17.68	15.6	6
10	69	32,829	1537	18.5	3.39	15.11	18.3	5
15	69	31,632	985	16.15	2.46	13.69	15.2	5
20	69	31,358	713	15.17	3.44	11.73	22.6	5
30	69	27,658	443	13.8	3.45	10.37	24.97	5
40	67	26,023	316	13.25	3.57	9.67	13.25	5
50	67	20,855	248	12.59	3.61	8.98	28.71	4

the analysis because affected by unsuitable sequences, and (3) an increased variability of each sampling unit composition (due to the presence of several bottom types in large sampling units) (Table 1). A 5 m^2 sampling unit size was chosen as the best balance between the inertia explained by environmental factors, and the number of megabenthic assemblages identified (Table 1). This size exceeds those previously used for shallow Mediterranean environments (e.g. Weinberg, 1978; Coppari et al., 2016), probably due to the wider range of environmental gradients and the much larger number of species included in this study.

Using 5 m^2 sampling units, a total of 38,230 organisms belonging to 69 megabenthic species were considered in the analysis (Table 1). Crinoidea, exclusively represented by the species *Leptometra phalangium*, was the most abundant and the third most frequent class accounting for 31.8% of all observed organisms, occurring in 16.3% of all sampling units (Table 2). Demospongiae, represented by 21 species (Supplementary material 3), was the second most abundant and the second most frequent class, accounting for 30.9% of all observed organisms, in 27.7% of all sampling units (Table 2). The class Anthozoa, represented by 27 species (Supplementary material 3), was the third most abundant and the first most frequent class, accounting for 21% of observed organisms, in 29.8% of all sampling units (Table 2). The remaining taxa were represented by 1–4 species (Supplementary material 3), accounting for 0.02–8.2% of observed organisms, in 0.2–14.5% of all sampling units (Table 2).

In the CCA performed using 5 m^2 sampling units, environmental factors explained 15.6% of the variation in species abundance. The first axis (CCA1) explained 26.8% of the variance, and the second axis (CCA2) explained 22.7% of the variance. Substrate was the best predictor (inertia = 2.19) followed by depth (inertia = 1.30), and slope (inertia = 0.70). Six different megabenthic assemblages (Fig. 2a), associated with different environmental factors (Fig. 2b) and most contributing species (Fig. 2c) were identified in the CCA analysis, for which illustrative in in situ pictures (Fig. 3), geographic (Fig. 4) and bathymetric distribution (Fig. 5) are also provided:

Table 2
Megabenthic taxa occupancy and abundance in the study area. Occupancy (frequency of occurrence in the set of sampling units); abundance (number of organisms).

Phylum	Class	Species number	Occupancy		Abundance	
			Number	(%)	Number	(%)
Porifera	Demospongiae	21	936	27.76	11,805	30.96
Cnidaria	Anthozoa	27	1004	29.8	8031	21
	Hydrozoa	3	14	0.42	16	0.04
Bryozoa	Gymnolaemata	1	31	0.92	47	0.12
Brachiopoda	Rhynchonellata	1	467	13.85	3219	8.20
Annellida	Polychaeta	4	491	14.56	2334	6.12
	Echiura	1	49	1.45	55	0.14
Echinodermata	Crinoidea	1	549	16.28	12,126	31.8
	Ophiuroidea	1	64	1.90	416	1.09
	Echinoidea	4	127	3.77	144	0.38
	Holothuridae	2	15	0.44	15	0.04
	Astroidea	1	11	0.33	12	0.03
Chordata	Ascidiacea	2	4	0.18	10	0.02

Assemblage A: occurred on shallow (95–110 m depth) maërl beds alternated with small patches of coralligenous outcrops (Fig. 2b), it was mostly characterized by the sponges *Haliclona* cf. *elegans* and *Aplysina cavernicola* (Figs. 2c, 3a and b and Supplementary material 4). Assemblage B: occurred on horizontal grounds covered by fine and coarse sands throughout most of the explored depth range (110–280 m depth) (Fig. 2b), it was mostly characterized by the presence of the crinoid *Leptometra phalangium* (Figs. 2c, 3c and Supplementary material 5). Assemblage C: occurred on horizontal grounds covered by medium sand to gravel from shallow to deep (110–330 m depth) environments (Fig. 2b), it was characterized by the presence of the brachiopod *Gryphus vitreus* (Figs. 2c, 3d and Supplementary material 6). Assemblage D: mostly found at shallow and intermediate depth (95–140 m depth) on mixed cobbles and pebbles bottoms (Fig. 2b), it was characterized by the polychaete *Salmacina dysteri* and two unidentified sponge species belonging to the genus *Hamacantha* and *Haliclona* (Figs. 2c, 3e, f and Supplementary material 7). Assemblage E: occurred on sloping rocky outcrops from shallow to deep environments (95–337 m depth) (Fig. 2b), it was characterized by the presence of the gorgonians *Eunicella cavolinii*, *Viminella flagellum*, the soft coral *Nidalia studeri*, the solitary coral *Thalamophyllia gasti* and the incrusting sponge *Hamacantha falcula* (Figs. 2c, 3g–k and Supplementary material 8). Assemblage F: occurred on vertical rock outcropping mostly at shallow and intermediate (95–210 m depth) environments (Fig. 2c), it was characterized by an encrusting sponge of the genus *Rhabderemia* (Figs. 2c, 3l and Supplementary material 9).

3.2. Spatial and bathymetric distribution of megabenthic assemblages

Assemblage A was only observed in one single transect in the north eastern side of the Menorca Channel (Fig. 4) and presented the narrowest bathymetric distribution (95–110 m depth) (Fig. 5). Assemblages B and C were widely distributed in both the northern and southern areas of the channel occurring between 110 and 180 m depth and between 110 and 240 m depth, respectively (Fig. 4). Assemblage D was observed in only four locations in the channel, three in the northern side and one in the head of the Menorca Canyon (Fig. 4), and partially coincided with assemblages A, E and F. This assemblage was distributed between 95 and 140 m depth (Fig. 5). Finally, assemblages E and F mostly co-occurred in transects located in the proximity of Cap Formentor and the Menorca Canyon's head (Fig. 4). However, assemblage E presented a shallower distribution compared to assemblage F that reached the deepest areas of the channel (340 m depth) (Fig. 5).

3.3. Variation of megabenthic diversity with depth

The highest species turnover was found in the shelf edge (110–180 m depth), followed by the outer continental shelf (90–110 m depth) and continental slope (180–347 m depth) (Fig. 6). Both shelf edge and continental slope species accumulation curves reached asymptote, highlighting that both depth ranges were representatively

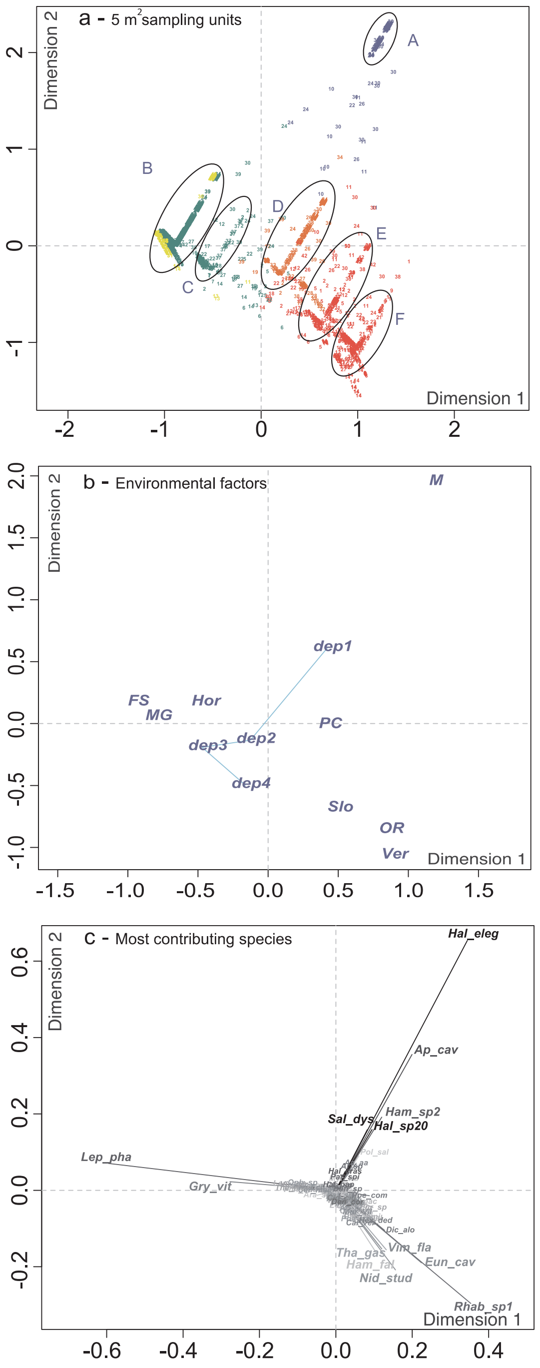

Fig. 2. Canonical correspondence analysis (CCA) ordination biplots of megabenthic species. In a) the biplot shows the distribution of the sampling units (n = 3372), sampling units are colored according to the dominant substrate: fine sands (yellow), medium sands to gravels (green), cobbles and pebbles (orange), maërl (blue), outcropping rock (red). In (b) the biplot shows the substrate type (FS = fine sands, MG = medium sands to gravels, PC = cobbles and pebbles, M = maërl, OR = outcropping rock), seabed slope (Hor = horizontal, Slo = sloping, Ver = vertical) and depth, being dep1 the shallowest and dep4 the deepest. In (c) the biplot shows the contribution of the different species to the megabenthic assemblages, the scale of greys in the vectors indicate the degree of correlation, being in black the highest correlation degree. Hal_eleg = *Haliclona* cf. *elegans*, Ap_cav = *Aplysina cavernicola,* Ham_sp2 = *Hamacantha* sp., Hal_sp20 = *Haliclona* sp., Sal_dys = *Salmacina dysteri,* Lep_pha = *Leptometra phalangium,* Gry_vit = *Gryphus vitreus,* Tha_gas = *Thalamophyllia gasti,* Ham_fal = *Hamacantha falcula,* Vim_fla = *Viminella flagellum,* Eun_cav = *Eunicella cavolinii,* Nid_stud = *Nidalia studeri,* Rhab_sp2 = *Rhabderemia* sp. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sampled. Conversely, species accumulation curve for the outer continental shelf did not reach an asymptote as a consequence of limited sampling.

3.4. Fishing activity in the study area

A total of 34 fishing vessels from eleven ports trawled the Menorca Channel's seafloor from January 2007 to July 2012, according to VMS data. Vessels from the ports of Cala Ratjada, Alcúdia and Ciutadella (Fig. 7) accounted for 80.3% of the VMS fishing events. One large (5) and two small (3 and 4) hot spot areas of bottom trawling were identified on the continental shelf of the channel at 50–75 m depth (Fig. 7). Four additional small and large hot spots were identified deeper on the continental slope in the north (1) and south openings (6, 7 and 8) of the channel at 500–600 m depth (Fig. 7). Finally, a small hot spot area was also observed near Cap Formentor (2) at ~50 m depth (Fig. 7). Three hot spots (1, 5 and 7) concentrated 73% of the total bottom trawling fishing effort in the area. None of the video transects considered in this study are located in the VMS hot spot areas (Fig. 7).

4. Discussion

The six megabenthic assemblages identified in the study area are distributed throughout the outermost continental shelf and upper slope of the Menorca Channel, and are mainly segregated by substrate type and depth.

Sponge grounds composed by large demosponge species (> 15 cm in height), mostly characterized by the branched *Haliclona* cf. *elegans* and the tubular sponge *Aplysina cavernicola* (Assemblage A), occur on a shoal located near the shelf edge off Cap Formentor at 95–110 m depth (Fig. 4). This shoal presents a highly irregular topography produced by vertical walls alternating with areas covered by maërl and coralligenous outcrops. The close proximity of the shoal to the shelf edge (Fig. 4), and its highly irregular topography, may represent favourable conditions for the development of sponge grounds, as already observed in the Mediterranean Sea (Bertolino et al., 2015) and in other areas of the world (e.g. Klitgaard and Tendal, 2004; Maldonado et al., 2016). In fact, it has been suggested that the irregular topography of these environments cause the acceleration of local currents (Rice et al., 1990) potentially favouring the presence of sponges (Beazley et al., 2015). *A. cavernicola* and *H.* cf. *elegans* account for 73% of all observed organisms, followed by other demosponge species such as *Poecillastra compressa, Aaptos aaptos* and *Siphonochalina* sp., representing 21% of the observed organisms. Species composition resembles that of other sponge grounds from flat rocky shoals exposed to moderated currents, and high silting (derived from river discharge), between 70 and 130 m depth in the Gulf of Santa Eufemia (southern Tyrrhenian Sea) (Bertolino et al., 2015). Overall, sponge density (9.2 ± 8.4 individuals m^{-2} (mean ± SD), max = 43 individuals m^{-2}) is similar to those observed in other Mediterranean sponge grounds (Bo et al., 2011a), exceeding those observed in deep multispecific sponge grounds in the North Atlantic (Kutti et al., 2013; Howell et al., 2016). The lack of gorgonians (only represented by a few colonies of *Paramuricea macrospina*) and antipatharians distinguishes this assemblage from Assemblage E, in which almost all the same sponge species (except *A. cavernicola*) co-occur together with large gorgonians and antipatharians (see below) (Supplementary material 3).

Leptometra phalangium beds (Fig. 3c) are widely distributed between 110 and 250 m depth in areas covered with both coarse and fine sands (Assemblage B), agreeing with previous reports from detritic bottoms of the Western Mediterranean shelf edge (e.g. Pérès, 1967; Michez et al., 2014). *L. phalangium* may reach very high densities of more than 30 individuals m^{-2} (5.3 ± 3.2 individuals m^{-2} (mean ± SD)), as previously observed on detritic substrates at the foot of seamounts in the Tyrrhenian Sea (Bo et al., 2010). In the Menorca Channel, this almost monospecific assemblage (*L. phalangium* represents 95% of all observed

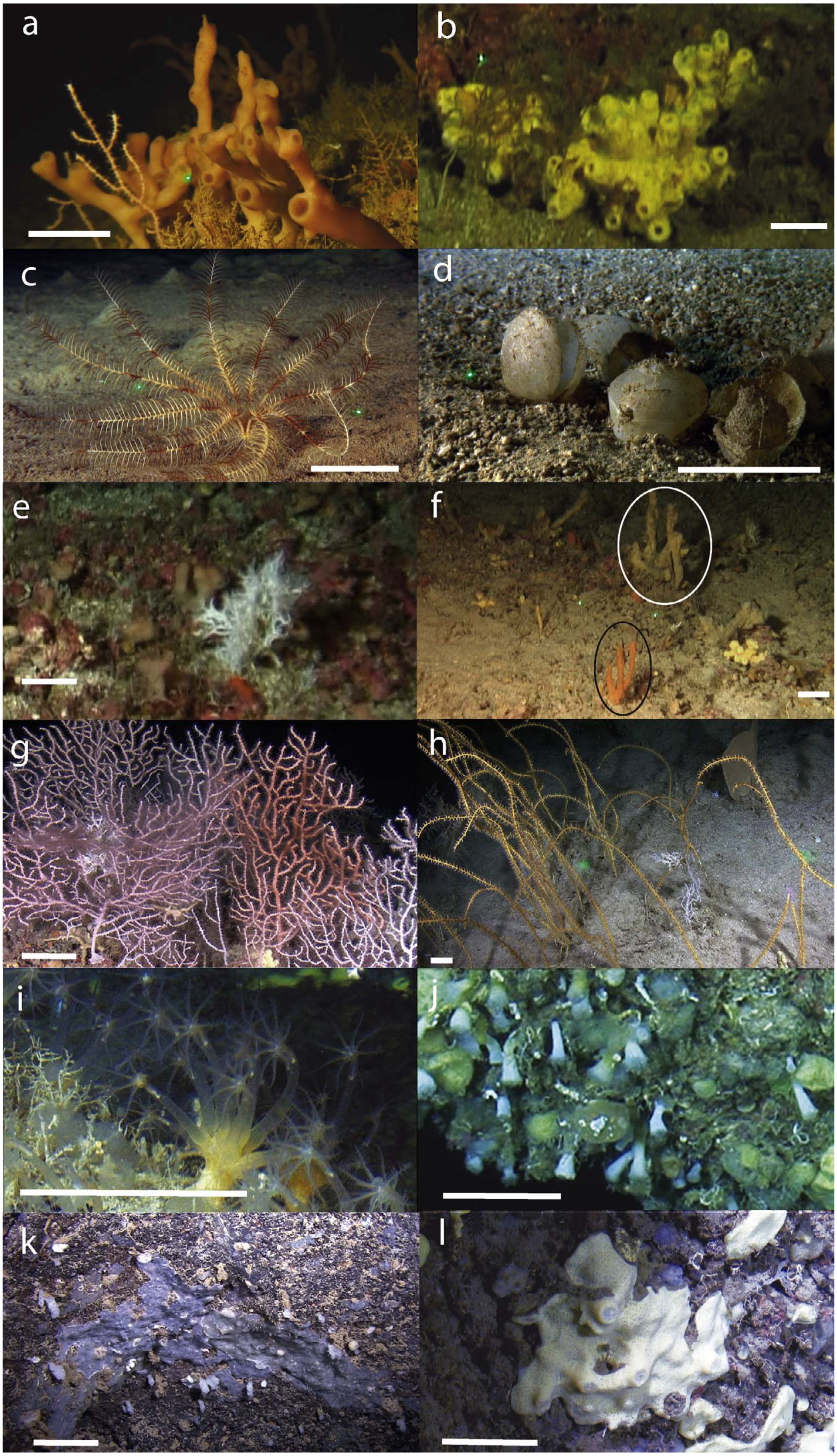

Fig. 3. Most contributing species to the CCA (a) *Haliclona* cf. *elegans*, (b) *Aplysina cavernicola*, (c) *Leptometra phalangium*, (d) *Gryphus vitreus*, (e) *Salmacina dysteri*, (f) *Hamacantha* sp. 2 (white circle) and *Haliclona* sp. 1 (black circle), (g) *Eunicella cavolinii*, (h) *Viminella flagellum*, (i) *Nidalia studeri*, (j) *Thalamophyllia gasti*, (k) *Hamacantha falcula*, (l) *Rhabderemia* sp. Scale Bar: 5 cm.

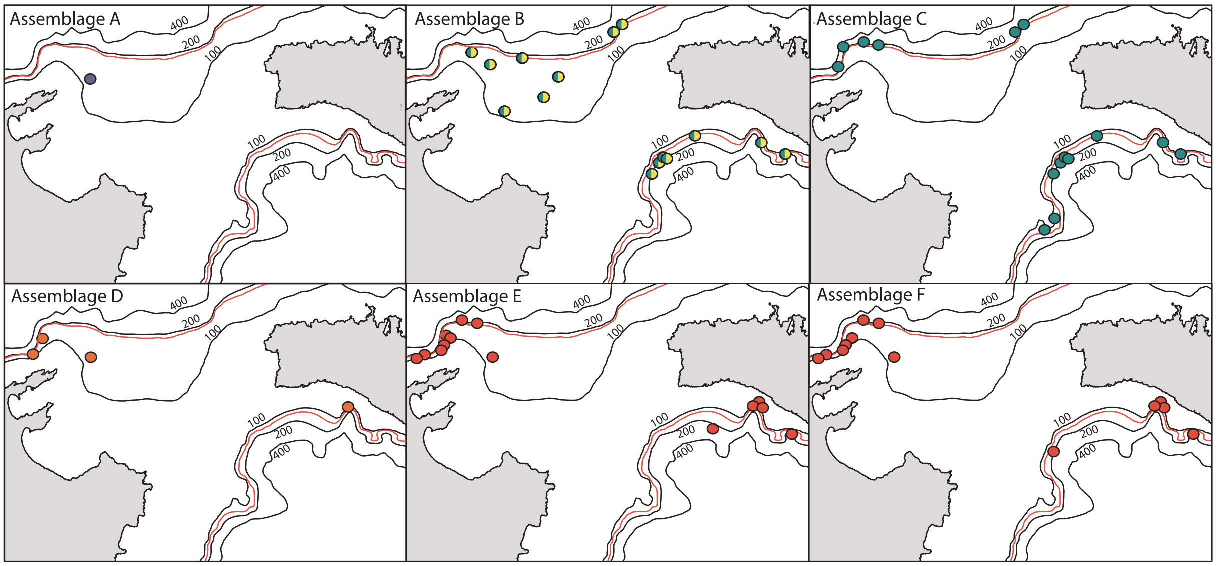

Fig. 4. Spatial distribution of megabenthic assemblages observed in the study area. Assemblages were represented on the study area based on the transects where they occur, and following the colours as in Fig. 2a. Grey line represents the 100, 200 and 400 m isobath, red line represents the shelf edge. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

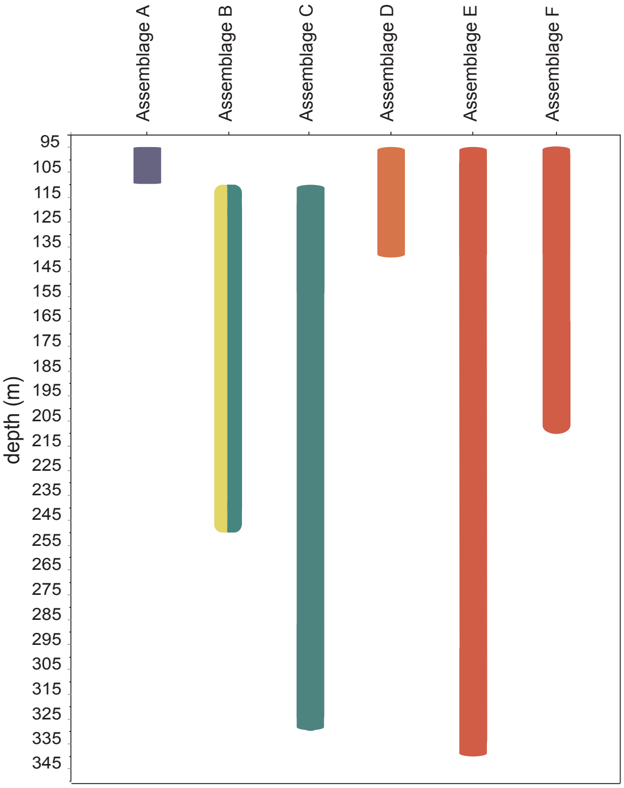

Fig. 5. Bathymetric distribution of the megabenthic assemblages observed in the study area. Assemblages were represented based on the colour as in Fig. 2a. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

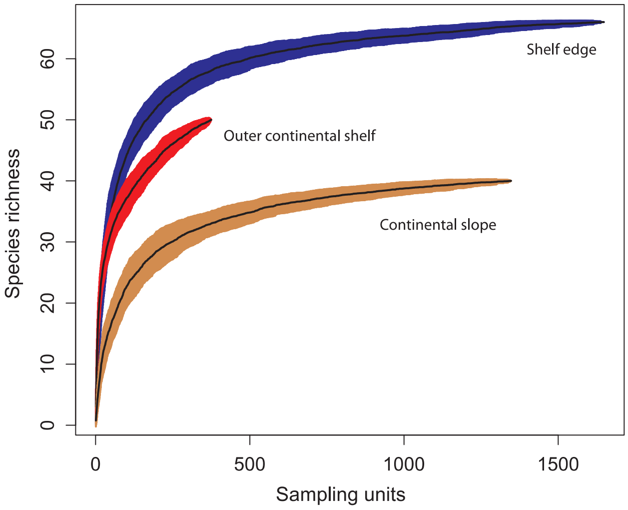

Fig. 6. Mean species accumulation curve calculated for the outer continental shelf (red), the shelf edge (blue) and the continental slope (orange). Colored areas around the curves represent the confidence intervals form standard deviation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

organisms) mostly occurs on the shelf edge (96% of occupied sampling units) (Fig. 4), in agreement with studies identifying it as a typical shelf edge assemblage (e.g. Fredj, 1964; Kallianiotis et al., 2000; Mangano et al., 2010). It has been suggested that *Leptometra* beds are mainly constrained to shelf edge environments as they depend upon the exposure to bottom currents that regularly carry high concentrations of suspended organic particles (Lavaleye et al., 2002; Colloca et al., 2003). Absence of trawling activity is fundamental for the persistence of high-density *L. phalangium* populations since the fragility of this organism makes it extremely vulnerable to mechanical damage (Smith et al., 2000). *L. phalangium* populations impacted by bottom trawling on the Cretan continental shelf presented significantly lower densities five months after trawling than non-impacted ones, suggesting a low recovering capacity (Smith et al., 2000). Facies of *L. phalangium* have been associated with elevated densities of benthopelagic fish, with high juvenile abundances, suggesting that this assemblage may play a crucial role in the life cycle of numerous fish species, some of which are of high commercial interest (e.g., *Merlucius merlucius* and *Mullus barbatus*) (Colloca et al., 2004). The sea pen *Funiculina quadrangularis*, the polychaete *Lanice conchilega* and the anemones *Cerianthus membranaceus* and *Arachnanthus oligopodus* accompany *L. phalangium* on coarse sands. In submarine canyons of the Western Mediterranean *C. membranaceus* and *F. quadrangularis* have also been reported to occur alongside facies of *L. phalangium* (Würtz, 2012). *F. quadrangularis* presents a sparse distribution and occurs at low densities (0.6 ± 0.3 colonies m^{-2}

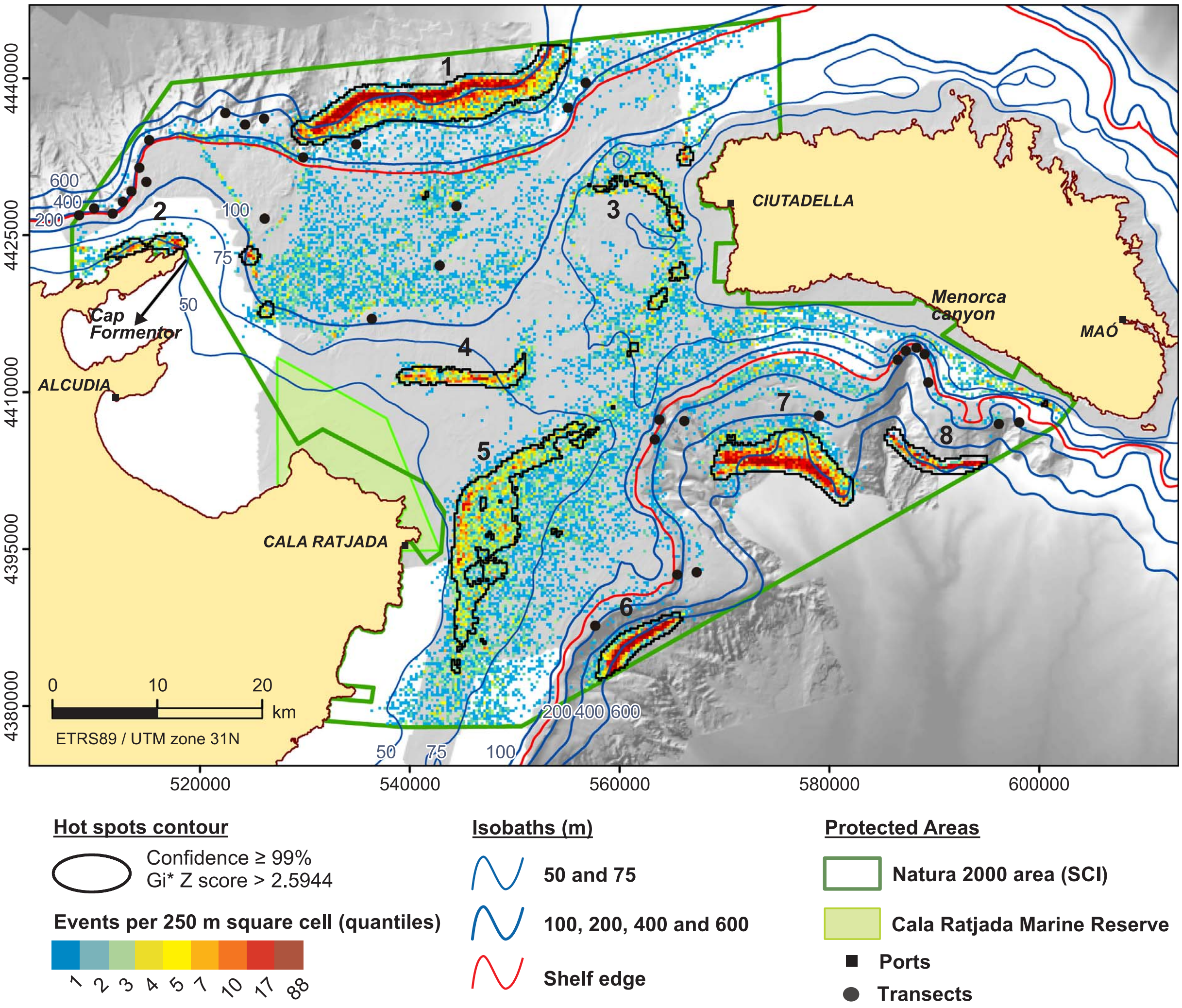

Fig. 7. Bottom trawling effort in the Menorca Channel. Colours refer to different trawling effort (see legend) and hot spot areas (identified using the Gi* statistic) are surrounded in black lines and indicated by capital letters. Video transects are represented by black dots, and the area included in the Natura 2000 network is indicated by the green line. None of the video transects considered in this study are located in the VMS hot spot areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(mean ± SD), max = 2.5 colonies m^{-2}) contrasting with observations in bathyal environments, where this species forms dense facies (Pérès and Picard, 1964). In fine sand environments, *L. phalangium* generally occurs along with the sea pen *Virgularia mirabilis*, the soft coral *Alcyonium palmatum*, and the sponge *Thenea muricata*. The presence of *T. muricata* and *V. mirabilis* on the shelf edge (~130 m depth) is rather surprising, as both species have mostly been reported in deeper settings (e.g. Michez et al., 2014). On fine sand floors, large hydrozoans have been occasionally observed, such as *Nemertesia antennina*, *Nemertesia ramosa* or *Lytocarpia myriophyllum*, which co-occurred alongside with *L. phalangium* in agreement with previous observations in the Tyrrhenian Sea (Massi, 2005). However, these hydrozoans present very low abundances in the Menorca Channel (Supplementary material 3), in contrast with dense facies observed in other areas of the Mediterranean Sea (Pérès and Picard, 1964).

The brachiopod *Gryphus vitreus* (Fig. 3d) constitutes 81% of all observed organisms in Assemblage C. *G. vitreus* forms beds that sparsely cover (2 ± 3 individuals m^{-2} (mean ± SD)) sandy bottoms on and beyond the shelf edge, at 110–330 m depth. This bathymetric distribution contrasts with observations from Corsica and Provence where *G. vitreus* beds reach a maximum depth of 200 m and 250 m, respectively (Emig, 1985, 1987). Conversely, communities dominated by *G. vitreus* have been reported in deeper environments of 660–870 m depth in the Balearic Basin (Cartes et al., 2009). In the upper slope, at 180–200 m depth, *G. vitreus* forms dense aggregations with more than 25 individuals m^{-2}. However, these densities are rather low if compared to those reported from continental slopes exposed to intense bottom currents (600 individuals m^{-2}) (Emig, 1987). In this regard, occurrences and abundances of *G. vitreus* and other brachiopods appear to be directly related to hydrodynamic conditions (Eshleman and Wilkens, 1979; Emig, 1987).

In the study area, *G. vitreus* beds (assemblage C) and *L. phalangium* facies (assemblage B) present similar distributions, occasionally co-occurring for tens of meters as previously shown in the Balearic Archipelago (Aguilar et al., 2014). However, while facies of *L. phalangium* (Assemblage B) have been observed on both fine and coarse sands, *G. vitreus* beds (Assemblage C) are basically restricted to coarse sands (Figs. 2 and 4). This substrate segregation responds to the necessity of *G. vitreus* to attach to small pebbles or shells on the seafloor (Emig, 1987). The composition of accompanying species in coarse sands of assemblage B and C is very similar, with the sea pen *F. quadrangularis*, the polychaete *L. conchilega* and the anemones *C. membranaceus* and *A. oligopodus* amongst the most abundant. *A. oligopodus* and *L. conchilega* have often been reported in soft sediments of the shelf edge and continental slope of the Mediterranean Sea (e.g. Pérès and Picard, 1964; Emig, 1997). On *G. vitreus* beds of the Menorca Channel, both species occasionally reach high densities (9.5 and 9 individuals m^{-2}, respectively), agreeing with previous observations in the Western Mediterranean Sea (Aguilar et al., 2014; Michez et al., 2014). The accompanying species reported in assemblage C differ from those observed in deeper *G. vitreus* beds in the Balearic Basin, which are accompanied by several sponge species and nemerteans (Cartes et al., 2009).

The polychaete *Salmacina dysteri* (Fig. 3e) and two unidentified sponges belonging to the genus *Hamacantha* and *Haliclona* (Fig. 3f) characterize Assemblage D, occurring on coarse sand with scattered cobbles and pebbles, at 95–140 m depth. These three species represent 63% of all observed organisms, and rarely exceed densities of 1.5 individuals m^2. Despite the mixed substrate where this assemblage has been observed, the vast majority of the organisms are associated with hard substrates (e.g. the sponges *P. compressa, A. aaptos* and *Pachastrella monilifera* (26% of observed organisms), and the gorgonians *E. cavolinii* and *Swiftia pallida* (10% of observed organisms)). A similar situation has been identified in sandy bottoms with *Dendrophyllia cornigera* coral rubble, which also present high abundances of organisms associated to hard substrates (Michez et al., 2014). Conversely, coarse sand patches are mainly occupied by echinoids, holothurians and polychaetes (1% of observed organisms). Isolated individuals of *L. phalangium* have been occasionally observed as well. The occurrence of Assemblage D in the same transects than Assemblages A and E (Fig. 4) (mainly in the immediate proximities of outcropping rocks and vertical walls on the shelf edge, and in areas of dead maërl rhodolites in the proximities of shelf shoals) suggests that Assemblage D is a transition between assemblages occurring on hard substrates and those located on coarse sand ones.

The gorgonians *E. cavolinii* and *Viminella flagellum*, the soft coral *Nidalia studeri*, the small solitary coral *Thalamophyllia gasti* and the incrusting sponge *Hamacantha falcula* (Fig. 3g–k) characterize (43% of all observed organisms) the sloping rocky substrates (Assemblage E) from the outer continental shelf to the upper slope (95–340 m depth). Despite this wide bathymetric distribution, this coral garden assemblage (*sensu* Stone, 2006; Buhl-Mortensen and Buhl-Mortensen, 2013) mostly occurs on the shelf edge and uppermost slope at 110–190 m depth (72% of observed sampling units), on rocky outcrops and vertical walls near Cap Formentor and at the Menorca Canyon head (Fig. 4). Similarly, other coral gardens have also been observed in the proximities of the shelf edge in several locations of the Western Mediterranean Sea (e.g. Bo et al., 2012; Cau et al., 2017). These environments are most likely exposed to regular currents, which may enhance food availability for large sized passive suspension feeders that characterize this assemblage (Shepard et al., 1974; Balbín et al., 2012). Both gorgonians *E. cavolinii* and *V. flagellum* had previously been reported as dominant species of rocky assemblages on the Mediterranean shelf edge (Bo et al., 2011b; Angiolillo et al., 2014). In the Menorca Channel, both species mostly form mixed assemblages along with other species (Grinyó et al., 2016), but they can punctually form dense monospecific patches of more than 20 colonies m^{-2}, as also observed in other areas of the Mediterranean Basin (Pedel and Fabri, 2011; Angiolillo et al., 2014). *N. studeri* and *T. gasti* form dense monospecific assemblages (30 colonies m^{-2}), the former mostly occurs on gently sloping rocky outcrops, the latter occurs on steeply sloping rocky outcrops. The incrusting sponge *H. falcula* shows low maximum densities of 5 individuals m^{-2} but of large size ($>$ 20 cm diameter), covering large areas of the rocky bottom, and perhaps excluding other species (Fig. 3k). Assemblage E is the most diverse of the six megabenthic assemblages identified in the study area. Eighteen species of demosponges have been observed as accompanying species (25% of all observed organisms) mostly as scattered individuals spread throughout the transects (2.4 ± 4 individuals m^2 (mean ± SD)), only occasionally reaching high densities (15 individuals m^{-2}). Some of these sponges reach large dimensions ($>$ 20 cm height and width) such as the massive *Haliclona magna* or the fan shaped *Phakellia robusta*, *P. monilifera* and *P. compressa*. Anthozoans account for 57% of all observed organisms in Assemblage E, with 22 different species. Besides *E. cavolinii* and *V. flagellum*, eight gorgonian species have been also observed in this assemblage: *Acanthogorgia hirsuta*, *Bebryce mollis*, *Callogorgia verticillata*, *Corallium rubrum*, *Muriceides lepida*, *Paramuricea clavata*, *P. macrospina,* and *S. pallida*. Gorgonians formed multispecific high-density patches ($\sim$20 colonies m^{-2}) (Grinyó et al., 2016), which contrasts with the lower gorgonian diversity in coastal and bathyal environments of the Mediterranean Sea (e.g. Gori et al., 2011; Cartes et al., 2013). The antipatharians *Antipathella subpinnata*, *Antipathes dichotoma* and *Leiopathes glaberrima* occur in low densities (1–4 colonies m^{-2}) in mixed assemblages with gorgonians, as also observed at similar depths in other areas of the Mediterranean Sea (e.g. Bo et al., 2009, 2012; Deidun et al., 2014). Finally, the recently described soft coral *Chironephthya mediterranea* (López-González et al., 2015) and *Paralcyonium spinulosum* are also largely represented in these rocky bottoms. Very similar anthozoan assemblages have also been described at similar depths on rocky substrates in the southern Sardinian shelf edge (Cau et al., 2017). Due to the complex three-dimensional structure they form, and the slow growth of gorgonian and antipatharian species (Sherwood and Edinger, 2009), deep coral gardens are extremely vulnerable to physical damage by fishing, (Angiolillo et al., 2015) and pollution (Silva et al., 2015), displaying extremely slow recovery (Althaus et al., 2009).

Finally, vertical rocky substrates at 95–210 m depth are dominated by encrusting sponges (Assemblage F), with an unidentified encrusting sponge of the genus *Rhabderemia* (Fig. 3l) accounting for 64% of all observed organisms (max = 23 individuals m^{-2}), and other encrusting sponges representing 10% of all observed organisms. Incrusting sponges seem to be the only organisms adapted to colonize this environment, alternating with the conversely highly diverse coral gardens (Assemblage E), depending on the substrate slope.

Differently form what reported in areas of the Gulf of Lion (Pérès and Picard, 1964; Orejas et al., 2009; Gori et al., 2013; Fabri et al., 2014) and the Catalan margin (Lastras et al., 2016), only a few colonies of the cold-water coral *Madrepora oculata* have been observed on vertical rocky walls at 320 m depth in the Menorca Channel. This could suggest that this species might be restricted to deeper environments in the study area ($>$ 350 m depth), as observed in other places of the Mediterranean Basin (e.g. Etiope et al., 2010; Taviani et al., 2015).

Benthic communities in the shallow area of the Menorca Channel have been also classified according to the European Nature Information System (EUNIS) (Barberá et al., 2012) and the "Lista Patrón de los Hábitats Marinos Presentes en España" (LPHME) (Moranta et al., 2014). Amongst the deeper assemblages described in this study, *L. phalangium* beds (Assemblage B) correspond to the EUNIS facies "*L. phalangium* in Mediterranean communities of the shelf-edge detritic bottom" (A5.472) and the LPHME "*Leptometra phalangium* fields in bathyal grounds of the continental shelf edge" (04020403), whereas *G. vitreus* beds (Assemblage C) correspond to the EUNIS category "Communities of bathyal detritic sands with *G. vitreus*" (A6.31) and the LPHME category "Bathyal grounds in the continental shelf edge with *Gryphus vitreus*" (04020404). Sponge grounds (Assemblage A) can only be generically classified into the EUNIS "Maërl bed" category (A5.51) and the LPHME category "Infralitoral and circalitoral rhodolite and detritic grounds dominated by invertebrates with the predominance of sponges" (0304051303). The transition assemblage (Assemblage D) could fall within the EUNIS category of "Mosaics of mobile and non-mobile substrata in the circalittoral zone" (X33) and the LPHME "Infralitoral and circalitoral grounds with cobles and gravels" (030401). Classification into EUNIS categories for the hard-bottom assemblages described in this study could only be based on environmental parameters; conversely, LPHME categories are based on a wider range of environmental and biological parameters allowing a more precise categorization. Coral gardens (Assemblage E) and vertical walls (Assemblage F) would both be classified as EUNIS "Rocky substrates in circalittoral" (A4.2) and "Deep-sea bedrocks" (A6.11) and as LPHME "Escarpments, walls and rocky slopes of submarine elevations and canyons of the circalitoral floor with anthozoans (scleractinians, gorgonians and antipatharians)" (0302022901) and "Escarpments, walls and rocky slopes of submarine elevations and canyons of the circalitoral floor with sponges" (0302022902). These results highlight the limitations of EUNIS and the need to improve this classification system for Mediterranean benthic environments occurring below 100 m depth.

The highest megafaunal species richness and beta-diversity (i.e. species turnover) is observed in the shelf edge (Fig. 6). This pattern probably results from the synergy caused by habitat heterogeneity and hydrodynamic conditions along the shelf edge. Indeed, rocky outcrops and vertical walls alternate with soft sedimented bottoms of varying grain sizes over the shelf edge. Moreover, both passive and active suspension feeders may benefit from the stable environmental conditions and hydrodynamic processes that enhance particle suspension in the near-bottom water layers on the shelf edge (Thiem et al., 2006). It has also been suggested that the observed increase in megafauna diversity at intermediate depths may result from the merging of species with shallower and deeper distributions, causing a mid domain effect (Colwell and Lees, 2000) as previously observed for deep coral communities in the north Pacific (Stone, 2006;Matsumoto et al., 2007).

Benthic megafauna such as erect and massive sponges (Klitgaard and Tendal, 2004), gorgonians (Maynou and Cartes, 2012), antipatharians (Koslow et al., 2001) and crinoids (Smith et al., 2000), are extremely sensitive to bottom trawling fishing. Low trawling pressure at 100–500 m depth in the study area (Fig. 7) and the natural protection offered by rocky escarpments and vertical walls may explain the preservation of the observed high-density and high-diverse megafauna assemblages on the continental shelf edge. Bottom trawling on the continental shelf and edge (Watling and Norse, 1998) has probably fragmented megabenthic assemblages (Hall-Spencer et al., 2002), confining them to remote and inaccessible environments (Díaz et al., 2015; Bo et al., 2015). The observed complexity and high-diversity of benthic megafauna in the Menorca Channel, may represent a portray how benthic community may have been in several areas of the Mediterranean continental shelf and shelf edge before the cumulative impact of decades of bottom trawling. A good knowledge of the composition and distribution of deep benthic communities represents the imprescindible baseline for the establishment of effective management measures for the conservation and recovery of deep ecosystems in large marine protected areas such as the Menorca Channel. Although the establishment of these large protection zones may pose potentially challenging situations amongst stakeholders, economic benefits may eventually materialize, including the recovery of degraded fisheries (Pipitone et al., 2000) and the maintenance of ecosystem services (Balmford et al., 2002).

5. Conclusions

- Six megabenthic assemblages are distributed throughout the outermost continental shelf and upper slope of the Menorca Channel, being mainly segregated by substrate type and depth.
- Beds of the crinoid *Leptometra phalangium* and the brachiopod *Gryphus vitreus* dominate soft substrates.
- Sponges dominate hard substrates on the outer shelf, whereas gorgonians, corals and incrusting sponges dominate hard substrates on the shelf edge and upper slope.
- The highest diversity of megabenthic species, within the studied bathymetric range, is found in the shelf edge.
- Trawling pressure concentrates above 100 m depth and below 500 m depth; consequently, low trawling pressure between 100 and 500 m depth probably contributes to the preservation of the observed benthic assemblages.

Acknowledgements

The authors thank the crew of the R/V *García del Cid*, the JAGO team (J. Schauer and K. Hissmann) from IFM-GEOMAR (Kiel, Germany), the NEMO ROV pilot Gavin Newman. David Díaz, Andreu Santín, Maria Montseny, Anthi Oikonomou, Artemis Atsalaki, Guillem Corbera, Alejandro Olariaga, Enrique Isla, Carlos Dominguez-Carrio, and Toni Garcia for their advice and help during the oceanographic surveys and the video analysis. We would like to thank Pablo J. López-González (cnidarians), Maria Jesus Uriz (sponges), Rafael Sardà (polychaetes) and Mikel Zabala (bryozoans) for their help provided in the taxonomical identification. This work was funded by the European project LIFE+ INDEMARES "Inventario y designación de la red Natura 2000 en áreas marinas del estado español" (LIFE07/NAT/E/000732).

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.pocean.2018.02.002.

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