



Distribution patterns and demographic trends of demosponges at the Menorca Channel (Northwestern Mediterranean Sea)

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ARTICLE INFO

Keywords:

Sponges
Geographical distribution
Size distribution
ROVs
Marine protected areas
Benthos
Mediterranean Sea
Balearic Archipelago
Menorca Channel

ABSTRACT

Nowadays, there is still a huge lack of knowledge regarding the morphology and size structure of sponge populations and their possible ecological implications. This study assesses, by means of quantitative analyses of video transects and morphometric analyses on still photographs, the geographical, bathymetrical and size-structure distribution of the most relevant habitat-forming sponge species on the 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. Additionally, the influence of seafloor variables on the observed distribution patterns was evaluated. Highest sponge densities and abundances were concentrated in areas of high hydrodynamism, namely the rocky shoals offshore Cap Formentor and the Menorca Canyon's head. Most of the studied species were dominated by small to medium size classes, suggesting pulse recruitment events. A clear depth-zonation pattern has been observed, going from the inner continental shelf to the upper slope. At the same time, the continental shelf harbored the presence of diverse and contrasting growth morphologies, yet the biggest forms occurred at the shelf edge and the upper slope. This study highlights the presence of dense, well-preserved sponge populations in the Menorca Channel, and provides a baseline for their future monitoring once the MPA is declared, potentially serving as reference for other areas across the Atlanto-Mediterranean region.

1. Introduction

Sessile invertebrates that present a complex three-dimensional structure are commonly referred to as ecosystem engineers (Buhl-Mortensen et al., 2010; Hogg et al., 2010). The wide morphological variability these species possess increases habitat heterogeneity, provides shelter (Buhl-Mortensen et al., 2010) and reproductive grounds (Cook et al., 2008), enhances food availability (Calcinai et al., 2013), and enables inter-species associations with a vast range of organisms (Buhl-Mortensen et al., 2010; van Soest et al., 2012). In this sense, the level of structural complexity of the so-called “engineer species” has been positively correlated with the abundance and diversity of accompanying species (e.g. Graham and Nash, 2013). Thus, morphological analyses of marine sessile organisms appear to be considered an important prerequisite for ecological research on benthic communities (Kaandorp and Kübler, 2001).

Sponges are among the most common suspension feeders in marine benthic ecosystems (Gili and Coma, 1998; van Soest et al., 2012), inhabiting from intertidal to hadal depths (Maldonado et al., 2015). They

can grow in a myriad of shapes and forms (Boury-Esnault and Rützler, 1997; Bell et al., 2006; Ackers et al., 1992), ranging from excavating forms (Rosell and Uriz, 2002), thin sheets and crusts (George et al., 2018), “cushions” (Uriz and Bibiloni, 1984), massive or elaborated forms, like giant barrel sponges (McMurray et al., 2010), lamellate (Bo et al., 2012) or branching shapes (Abraham, 2001; Kaandorp and Kübler, 2001). This morphological variability results from a combination of intrinsic (genetically pre-determined) and extrinsic (biotic or abiotic) factors (Meroz-Fine et al., 2005). Initially, the sponge growth habit is conditioned by the shape of its internal skeleton and its composition (van Soest et al., 2012) yet, abiotic factors, such as hydrodynamism (Barnes, 1999), substrate inclination (Bell and Barnes, 2000a; 2000b), light (Sarà, 1964) and sedimentation rates (Bell and Barnes, 2000c) may alter the initial morphology of sponges. As so, the adaptability of a given growth shape or the capacity to adapt it to the environmental factors are closely linked to the organisms' survival in a given habitat (Vogel, 1994).

Sponge morphology has been proposed as an informative, inexpensive monitoring method for studying sponge assemblages (Bell

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and Barnes, 2000c; 2003; Bell et al., 2006; 2017). In the past decades, the monitoring of sponges through time has mostly been based on assemblage composition and the abundance of selected species (Bell et al., 2017). However, when conservation assessment over time is the purpose of monitoring, sponge abundance may not provide sufficient information (Bell et al., 2017) due to their long lifespan (Hogg et al., 2010) and sporadic recruitment episodes (Dayton et al., 2016). To fill this gap, morphological information can be obtained alongside species abundance data, providing an additional insight in relation to environmental factors and/or anthropogenic stressors that may influence the studied populations (Möller et al., 2019). Additionally, size-frequency distribution has also been proposed as an adequate tool to evaluate the state of a given population, with the shift towards smaller or bigger individuals being indicative of physical disturbance and/or recruitment success over time (Bell et al., 2017). Nevertheless, until now changes in sponge morphology have mostly been analyzed in SCUBA-accessible depths (Bell and Barnes, 2000a; 2000b; Meroz-Fine et al., 2005; Bell et al., 2006), often focusing on one single or few sponge species (Turón et al., 1998; Kaandorp and Kübler, 2001; McMurray et al., 2010; Coppari et al., 2016). Contrastingly, only a couple of studies have been performed on the outer continental shelf and slopes (Maldonado and Young, 1996; Bo et al., 2012).

Moreover, despite the prevalence of demography and size frequency distribution as descriptors for other benthic sessile organisms' monitoring, (Linares et al., 2008; Ambroso et al., 2013), they have barely been used on sponge populations (Bo et al., 2012). Consequently, information on the size frequency of most Mediterranean sponges is poorly documented, leaving a knowledge gap about the size structure of sponge populations and their possible ecological implications (Turón et al., 1998) and conservation relevance (Bo et al., 2012).

The Menorca Channel area is intended to be declared as a Marine Protected Area (MPA) in the near future, which has prompted extensive and intensive ROV surveys during past years in order to obtain an accurate description of the current status of megabenthic assemblages. So

far, studies have focused at community level (Barberá et al., 2012; Grinyó et al., 2018a) and on gorgonian populations (Grinyó et al., 2016; 2018b). Sponges, on the other hand, have only been recently characterized at the assemblage level (Santín et al., 2018), with information regarding their distribution, abundance, size-structure and morphology still undocumented.

The present study aims to provide a reliable and replicable starting point to enable the monitoring of sponge populations in the future MPA by: (1) assessing the geographical and bathymetrical distribution of the most relevant sponge species in the study area, (2) appraising their size-frequency distribution, (3) characterizing the morphology of the most common habitat-forming species, (4) investigating the possible environmental factors that may affect the above-mentioned variables.

2. Material and methods

2.1. Study area

The Menorca Channel is located between Mallorca and Menorca Islands ($39^{\circ} 53' 0.73''$ N, $3^{\circ} 29' 51.16''$ E) (Fig. 1) in the Balearic Archipelago (western Mediterranean Sea). The channel's continental shelf extends between both islands, at depths ranging from 40 m in its shallowest part to 180 m at the shelf break (Acosta et al., 2003). The shelf covers an approximate area of 2000 km² and is largely covered by soft sediments and maërl beds, with hard substrata restricted to scattered coralligenous outcrops (Druet et al., 2017). Soft sediments are the dominant substrate typology at the shelf edge (110–180 m depth) and slope, with the exception of Cap Formentor (Fig. 1a) and the Menorca Canyon's head (Fig. 1b), which are characterized by rocky outcrops and vertical walls. In addition, the absence of fluvial outputs confers high transparency to the water column (Canals and Ballesteros, 1997), resulting in elevated light intensity values across the entire shelf (Ballesteros, 1994).

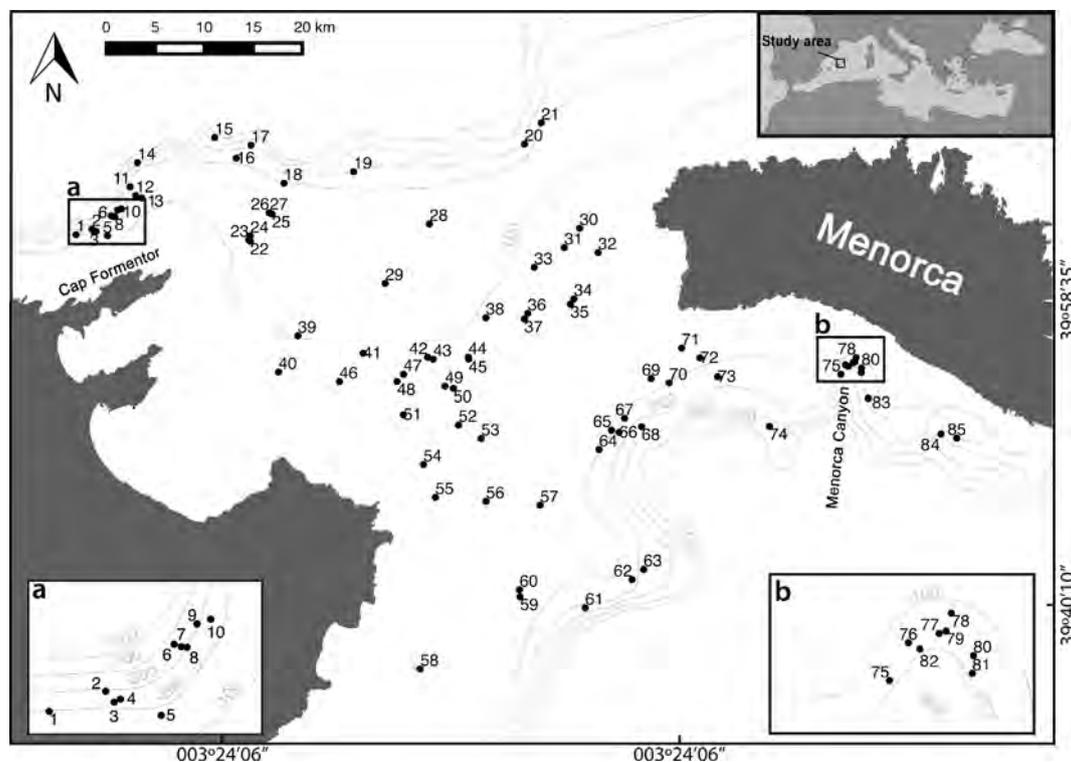


Fig. 1. Location of the video transects in the study area. (a) Zoom showing video tracks 1–10 in Cap Formentor. (b) Zoom showing video tracks 75–82 in the Menorca Canyon's head. Projected view (UTM Zone 31N (WGS84)) with geographic (WGS84) coordinates indicated for reference. The location of the survey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

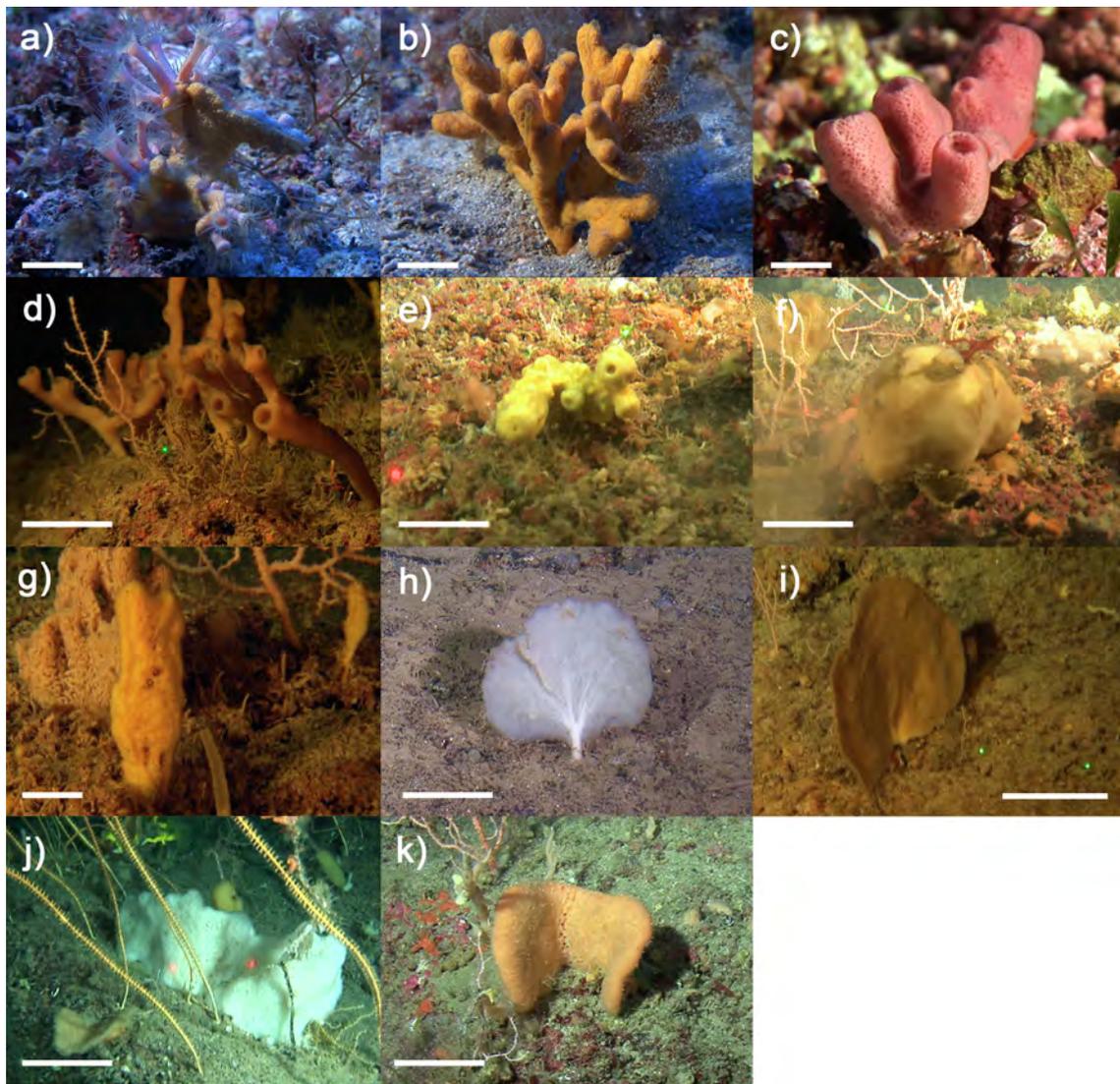


Fig. 2. Close up of the selected species: (a) *Axinella damicornis* with *Parazoanthus axinellae*, (b) *Axinella verrucosa*, (c) *Haliclona (Reniera) mediterranea*, (d) *Haliclona cf. elegans*, (e) *Aplysina cavernicola*, (f) *Aaptos aaptos*, (g) *Dictyonella alonsoi*, (h) *Phakellia robusta*, (i) *Phakellia hironellei*, (j) *Pachastrella monilifera* (white) and *Poecillastra compressa* (orange) alongside a facies of the octocoral *Viminella flagellum*, (k) *P. compressa*. Scale bars: 1 cm (a-c, g), 5 cm (d-g, h, j, k) and 12 cm (i) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

2.2. Selected sponge species

The identification of sponge individuals was achieved based on voucher individuals and HD photographic records obtained from the video images. Fragments of the voucher specimens were collected and used for spicular analyses in order to properly assess their identification (see Fig. 2).

The sponges species selected for this study (Fig. 2; Table 1) were chosen according to the following criteria: (1) they represented the main constituents of sponge assemblages in the area in terms of abundance and/or frequency (Santín et al., 2018) and (2) had a three-dimensional (3D) morphology. All lamellate sponges were also considered due to their paramount role on benthic communities (Bo et al., 2012).

All sponges were considered in the geographic and bathymetric distribution study, but only images of *A. aaptos*, *A. damicornis*, *A. verrucosa*, *D. alonsoi*, *P. compressa*, *P. monilifera*, *P. robusta* and *P. hironellei* were considered suitable for morphometric analyses, whereas *A. cavernicola*, *H. mediterranea* and *H. cf. elegans* were excluded because of their irregular shape and their high morphological variation between individuals. Additionally, and because of their aberrant or

undifferentiated morphology, *Axinella* spp. and *D. alonsoi* recruits could not be assigned to a given species and were left out of the analysis, with just a semi-quantitative estimate for each transect (Fig. 8).

2.3. Video recording and analyses

A total of 85 video transects (Fig. 1; see Supplementary material 1) were recorded during six surveys conducted with the research vessels (R/V) “García del Cid” (September 2010, April 2011, October 2011, June 2012), “Miguel Oliver” (August 2011) and “SOCIB” (August 2014). The first 20 video transects were recorded with the manned submersible “JAGO” (IFM-GEOMAR), whereas the remaining 65 video transects were recorded using the remotely operated vehicle (ROV) “NEMO” (Gavin Newman) during the last four campaigns. Both instruments were equipped with an high definition (HD) camera, depth sensors, a grabber and two parallel laser beams that provided a fixed scale used in the subsequent video analyses. Both JAGO and NEMO moved at a constant speed of ~0.3 knots, with transect lengths ranging between 80 and 2375 m, and over depths ranging from 50 to 360 m. All video transects were recorded in digital format.

Transects were haphazardly located along the study area in order to

Table 1

Selected sponge species for this study. The table includes the species' morphology and the different analyses performed on each species.

| Species | Main Morphology | Analyses performed | | |
|--|---|---|-------------------------|-----------------------------|
| | | Geographical and bathymetrical distribution | Morphometrical analyses | Size-frequency distribution |
| <i>Axinella damicornis</i> (Esper, 1794) | Arborescent, with compressed branches (lamellate) | X | X | X |
| <i>Axinella verrucosa</i> (Esper, 1794) | Arborescent, with cylindrical branches | X | X | X |
| <i>Haliclona (Reniera) mediterranea</i> Griessinger, 1971 | Massive-lobose, with oscular chimneys | X | – | – |
| <i>Haliclona cf. elegans</i> (Bowerbank, 1866) | Anastomosing branches (highly polymorphous) | X | – | – |
| <i>Aplysina cavernicola</i> (Vacelet, 1959) | Massive base with irregular tubular digitations | X | – | – |
| <i>Aaptos aaptos</i> (Schmidt, 1864) | From globular to massive forms | X | X | X |
| <i>Dictyonella alonsoi</i> Carballo, Uriz & García-Gómez, 1996 | Arborescent, with few branching processes | X | X [*] | X |
| <i>Pachastrella monilifera</i> Schmidt, 1866 | Lamellate; highly irregular | X | X | –** |
| <i>Phakellia hironellei</i> Topsent, 1890 | Lamellate; pedunculated | X | X | –** |
| <i>Phakellia robusta</i> Bowerbank, 1866 | Lamellate; pedunculated | X | X | X |
| <i>Poecillastra compressa</i> Bowerbank, 1866 | Mainly lamellate; rarely cup-shaped | X | X | X |

* Only high could be measured for *D. alonsoi*.

** Morphological measures were taken, however there were no population of either *P. hironellei* or *P. monilifera* that passed the 30 individuals threshold for the size-frequency distribution.

cover its whole extension, but areas presumably covered by rocky substrates were explored more intensively. Overall, a total distance of 64.2 km was video recorded.

Quantitative video analysis was performed following the methodology described by Gori et al., (2011), using Final Cut Pro 7 software (Apple Inc.). Pauses and loops were removed from the footage in order to avoid an overestimation of the transect length. Video sequences with poor image quality (e.g. recorded too far away from the sea floor) were discarded from the analysis. Once unsuitable fragments were removed, the remaining 93.4% of the video footage, which corresponded to a total distance of 64.2 km, was considered suitable for video analysis.

Every sponge observed within a width of 0.3 m along each video transect was assigned a time reference corresponding to the elapsed time since the beginning of the video transect to the intersection between the laser beams and each sponge individual. Substrate, depth and slope information (or characteristics) along the transects were also extracted from the videos following the methodology described in Grinyó et al. (2016).

Time reference was posteriorly transformed into a known position along the transect using the velocity of the vehicle ($P = t \cdot v$, where t is the time reference expressed in seconds, and v is the velocity expressed in meters per second). Transects were subdivided into 20 m² sampling units based on Santín et al. (2018), who determined that this was the minimal area suitable to properly characterize the sponge assemblages of the Menorca Channel.

HD still images for morphometric analysis were extracted directly from the ROV footage. Still images were extracted when laser-beams where in the same plane as the sponge, and sponges appeared in a frontal plain that allowed posterior measurements.

2.4. Geographical and bathymetrical distribution and relationship with environmental factors

Geographical distribution of each sponge species was studied by plotting the observed density values on a geographically referenced map created with the R software platform (R Core Team) using the packages *raster* (Robert, 2016), *sp* (Bivand et al., 2013) and *rgdal* (Bivand et al., 2017).

To evaluate the bathymetrical distribution, we subdivided our depth range (50–360 m depth) into 20 m depth intervals, and grouped all sampling units within each depth interval. Boxplots were then generated for each species' density values for each depth interval.

A canonical correspondence analysis (CCA) was used to test the relationships between sponge abundances and abiotic factors (i.e. depth, substrate type and slope) by means of the *vegan* package

(Oksanen et al., 2016) of the R software platform. The *anova* function (ANOVA test) of the same package was used to assess the significance of the selected factors. Sponge abundances were log transformed before running the tests.

2.5. Morphometric analyses and size-frequency distribution

In total, 1438 pictures were analyzed by means of the software Macnification v.1.8 (Orbicule) taking several morphometric measurements (height, width/diameter, perimeter) of the observed sponges (Fig. 6a–d). Then, the equation describing the morphometric correlations and their correlation coefficients was calculated for each species by means of the *fdth* library (Faria, et al., 2016), available at the R software platform. For *A. damicornis* and *A. verrucosa* perimeter was not evaluated due to their morphological plasticity, presenting several growth forms in both a 2D or 3D body plan (Pansini, 1984), which might compromise the overall shape of the individuals depending on the camera position (Munro, 2013).

Size structure of sponge populations, understood as all the individuals of a given species within a single transect, was analyzed in terms of size-frequency distribution histograms and distribution parameters, such as Skewness and Kurtosis. Only populations with more than 30 individuals were studied for their population size structure, as populations with lower values could compromise skewness and kurtosis estimates (Linares et al., 2008). Size-frequency histograms were produced for each species' population, and skewness and kurtosis were calculated by means of the R software platform functions *agostino.test* (Komsta and Novomestky, 2012) and *anscombe.test* (Anscombe and Glynn, 1983), available at the *moments* library. Skewness is a measure of the symmetry of a distribution based on its mean. If skewness is significant ($p < 0.05$), population size structure is asymmetrical, with positive values reflecting the dominance of small-size individuals and negative values denoting the prevalence of large individuals on a given population. Kurtosis is a measure of the peakedness of a distribution near its central mode. A significant kurtosis value ($p < 0.05$) indicates that particular size prevails in the population.

3. Results

3.1. Geographic and bathymetrical distribution

Regarding their geographical and bathymetrical distribution, *Axinella damicornis*, *A. verrucosa* and *Haliclona mediterranea* were exclusively restricted to the continental shelf, whereas *Phakellia hironellei*, *P. robusta* and *Pachastrella monilifera* were recorded exclusively

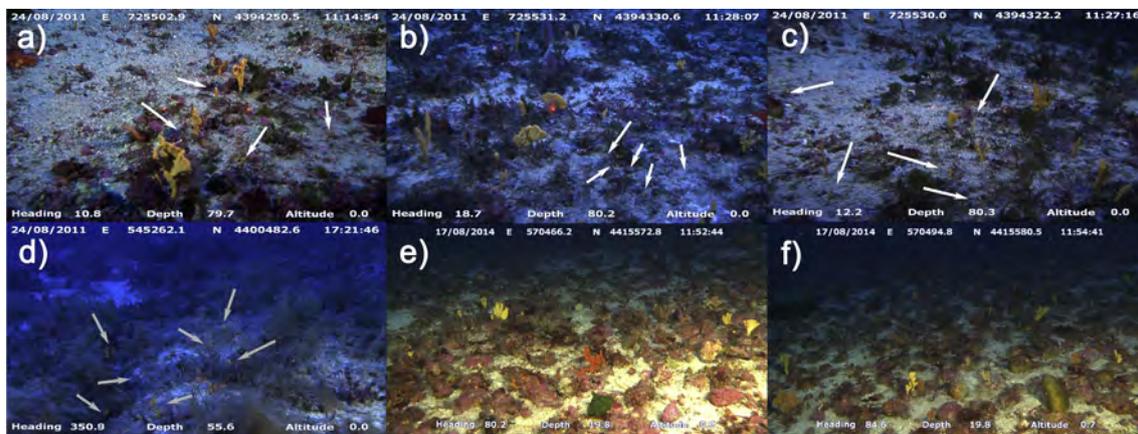


Fig. 3. Inner continental shelf coralligenous and rock formations with Axinellid assemblage: (a–c) *Axinella damicornis* (erect-flabellate) and *Axinella verrucosa* (erect-arborescent) occurring atop sub outcropping rocks at the inner continental shelf. White arrows signal the presence of *Axinella* buds. (d) *A. damicornis* individuals (grey arrows) partially or totally covered by turf-forming algae; (e, f) *A. damicornis* individuals occurring on rodolith and maërl beds of the southern continental shelf.

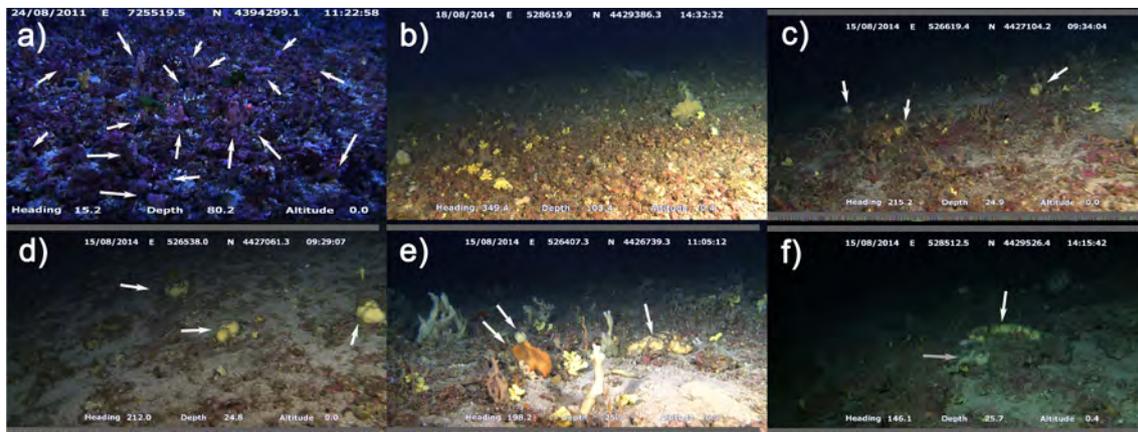


Fig. 4. Inner continental shelf's maërl beds with *Haliclona mediterranea* assemblage: (a) *H. mediterranea* (white arrows) monospecific patches occurring on maërl beds of the inner continental shelf. Outer continental shelf's sciaphilous communities dominated by “Haliclonid-Aplysina” assemblage: (b–c) *Aplysina cavernicola* (yellow) and *Haliclona cf. elegans* (pink) individuals occurring on maërl beds near Cap Formentor. White arrows indicate the presence of *Aaptos aaptos* spherical individuals; (d) Massive *A. aaptos* (white arrows), most likely due to the fusion of individuals resulting from asexual reproduction; (e) *H. cf. elegans* (pink) and *A. cavernicola* (yellow) alongside (white arrows): *Poecillastra compressa* (orange) and globular and massive *A. aaptos* individuals; (f) *A. aaptos* (white arrows) fused individuals in a “chain-like” pattern. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

on the shelf edge and upper slope area. *Aaptos aaptos*, *Aplysina cavernicola* and *H. cf. elegans* mostly occurred on the continental shelf, yet they could still be found with low densities at the upper limit of the shelf edge. Conversely, *Poecillastra compressa* and *Dictyonella alonsoi* mostly occurred at the shelf edge and upper slope, yet they were also recorded at the outer continental shelf, close to the shelf edge at the Cap Formentor area (Figs. 1; 7b).

Axinella damicornis and *A. verrucosa* shared geographical and bathymetrical distributions, both being mostly found at a depth of 50–90 m among the central continental shelf (Figs. 7a; 8a). *Haliclona mediterranea* was mostly found at the same depth range as the two *Axinella* (50–90 m), yet they seldomly co-occurred. *Haliclona cf. elegans*, *A. cavernicola* and *A. aaptos* mostly occurred at the outer continental shelf (70–110 m), and co-occurred at the northernmost part of the studied area, near Cap Formentor. On the contrary, at the southernmost part of the studied area these species were spatially displaced, with *A. cavernicola* and *A. aaptos* concentrating towards the Menorca Canyon and *H. cf. elegans* towards the south-central continental shelf. Finally, while *A. cavernicola* was mostly sparse at the upper limit of the shelf edge (110–150 m), one of its population was relatively dense at this depth range near the Menorca Canyon's head (Figs. 7a; 8a).

Dictyonella alonsoi populations mostly concentrated towards Cap Formentor (Fig. 7b), being more widely spaced at the southern slope. Yet, its densest populations were recorded in the southern area (Fig. 7b). Populations of *P. monilifera*, *P. hirondellei*, *P. robusta* and *P. compressa* were also mainly found at Cap Formentor, with a few southern populations concentrated close to the Menorca Canyon's head (Fig. 7b). Overall, *P. monilifera* and *P. hirondellei* presented lower densities than *P. compressa* and *P. robusta* at all sites. Regarding the latter, *P. compressa* presented its maximum density at Cap Formentor and *P. robusta* presented its maximum density at the Menorca Canyon's head (Fig. 7b). Regarding their bathymetrical distribution, *D. alonsoi* and all lamellate species predominantly occurred between 110 and 210 m depth (Fig. 8b), although *P. robusta* presented a density peak at 290 m.

3.2. Relationship with environmental features

Depth, substrate type and slope altogether explained ~ 37% of the total inertia (i.e. explained variation of the data) in the CCA. According to the ANOVA permutation test, the three factors contributed significantly ($p < 0.001$) to the ordination (Fig. 9). Depth clearly segregated sponges found on the continental shelf (*A. damicornis*, *A.*

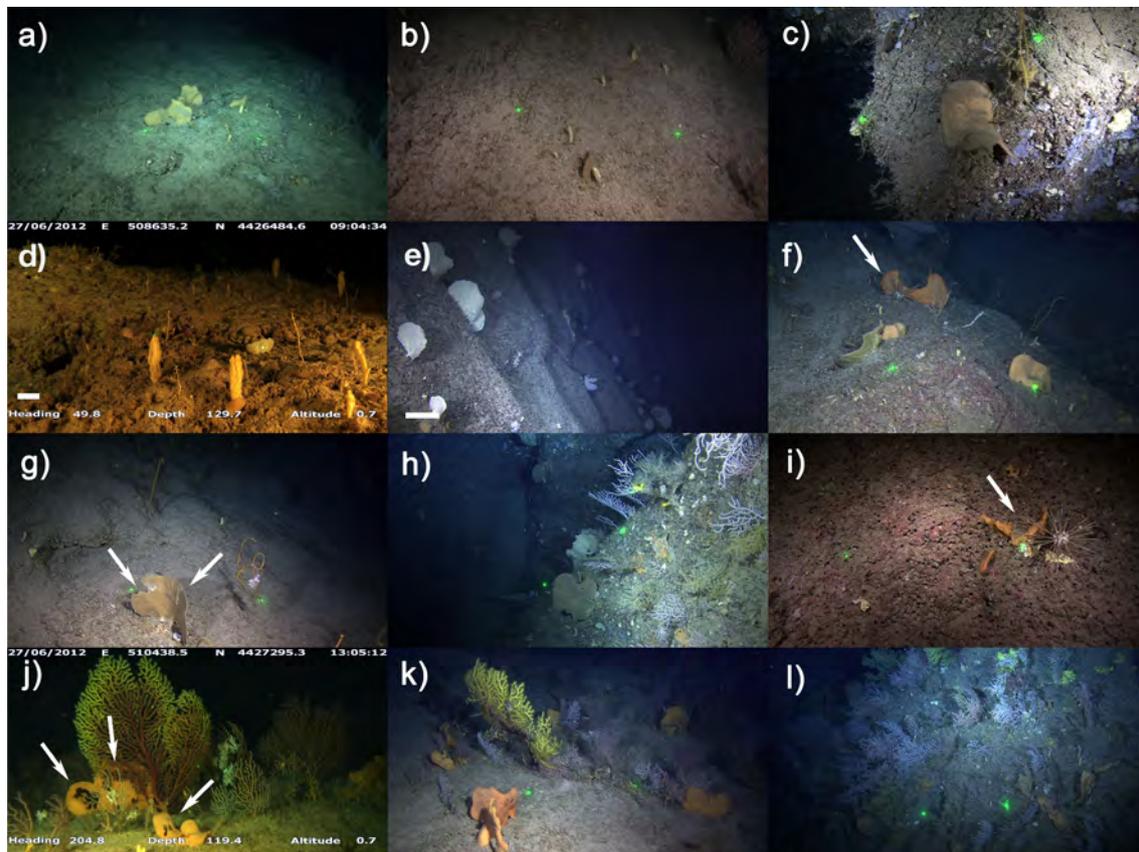


Fig. 5. Shelf edge and slope rocky bottoms with lamellate sponges: (a-b) *Poecillastra compressa* (orange) and *Dictyonella alonsoi* (dull-yellow) on horizontal rocky bottoms (170 m depth) (b) *D. alonsoi* (dull-yellow) individuals alongside the lamellate sponge *Phakellia hironellei* (dull-brown) (c) *P. compressa* growing alongside the encrusting sponge *Hamcantha (Vomerula) falcula* (bluish-grey) and the whip-like octocoral *Viminella flagellum* (orange) (d) Close up of a facies of *D. alonsoi* (e) Dense facies of *Phakellia robusta* growing on vertical walls (190 m depth) (f) *P. compressa* (orange), *P. hironellei* (dull-brown) and *D. alonsoi* (dull-yellow) over horizontal rocks. The sea urchin *Cidaris* sp. (white arrow) is shown next to a *P. compressa* individual with signs of grazing (g) *P. hironellei* with signs of damage (white arrow) alongside the whip-like octocoral *V. flagellum* (h) the lamellate sponges *P. robusta* (white) *P. hironellei* (dull-brown) inhabiting facies of the octocoral *Eunicella cavolinii* (grey-whitish) (i) *P. compressa* individuals growing on a vertical wall, with the biggest individual showing clear signs of heavy grazing activity by a cidarid (white arrow) (j-l) *P. compressa* (orange) individuals growing alongside mixed facies of octocorals, mainly *Paramuricea clavata* (yellow-violet), *Paramuricea macrospina* (eggplant) and *E. cavolinii* (white) at a depth range between 110 and 140 m. Some *P. compressa* individuals show damage caused by the interaction with the arborescent morphology of the gorgonians (white arrows). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

verrucosa, *A. cavernicola*, *A. aaptos*, *H. cf. elegans* and *H. mediterranea*) from those occurring at the shelf edge and the upper slope (*D. alonsoi*, *P. hironellei*, *P. robusta*, *P. monilifera*, and *P. compressa*). Additionally, species from the inner continental shelf (*A. damicornis*, *A. verrucosa* and *H. mediterranea*) were also segregated from those of the outer continental shelf (*A. cavernicola*, *A. aaptos* and *H. cf. elegans*). All continental shelf species were associated with horizontal substrates, whereas shelf edge and upper slope ones were associated with sloping and vertical surfaces. On the continental shelf, *Axinella* species were mainly associated with coralligenous and rocky outcrops, *H. mediterranea* was strongly associated with maërl beds, and *A. cavernicola*, *A. aaptos* and *H. cf. elegans* were associated mostly with maërl beds and cobbles and pebbles. All the studied species from the shelf edge and upper slope occurred on rocky outcrops.

3.3. Population size-structure and morphology

Overall, all equations describing the morphometric correlations between width, height and perimeter were similar for both massive-globular and lamellate sponges (Table 2). In most cases width/diameter vs. perimeter showed the highest correlation ($R^2 = > 90$), followed by height vs. width ($R^2 = > 70$), with height vs. perimeter ($R^2 = > 50$) showing the weakest correlation for all shapes (Table 2). On the

contrary, branching-erect sponges (*A. verrucosa* and *A. damicornis*) showed a weaker height vs. width correlation ($R^2 = \sim 60$) in all populations. Nevertheless, the coefficients of determination (R^2) were considerably higher ($R^2 = 65-80$) for both species when calculated for each population separately.

Size-structure analyses were performed on a total of 47 sponge populations (transects with > 30 individuals each; Table 3; Supplementary material 2), which corresponded to: *A. aaptos* (4), *A. damicornis* (10), *A. verrucosa* (8), *D. alonsoi* (13), *P. robusta* (5) and *P. compressa* (7). Most size-distributions were unimodal regardless of the species, with just a few exceptions (Figs. 10a; 10b). Size-distributions of *A. damicornis* populations were in general positively skewed, indicating a dominance of small to medium sizes classes. Most size-distributions of *A. verrucosa* populations were significantly skewed towards values close to 0, implying a dominance of intermediate size classes in almost all populations. Regarding kurtosis, over-centralized distributions were present in half the *A. damicornis* populations and just in one *A. verrucosa* populations. Size-distribution of all *A. aaptos* populations were positively skewed and mostly of them showed significant kurtosis, indicating a dominance of small to medium sizes classes with over-centralized size-distributions. All but one population of *D. alonsoi* were positively skewed, with only half of them showing significant kurtosis. The lamellate sponges *P. robusta* and *P. compressa* size-distribution was

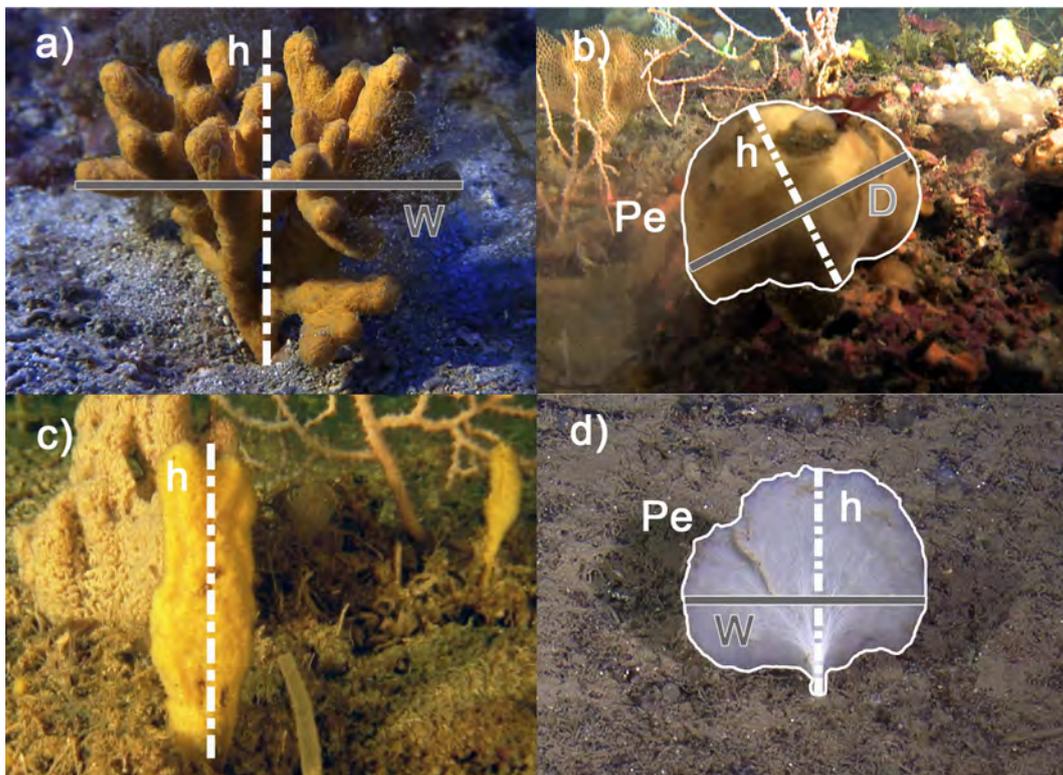


Fig. 6. Example of the evaluated morphometric parameters used in this study, height (h), width (W) or diameter (D) and perimeter (Pe) for: (a) branching-erect, (b) massive-globular, (c) erect and (d) lamellate morphologies. Species shown in pictures a-d are as follows: (a) *Axinella verrucosa*; (b) *Aaptos aaptos*; (c) *Dictyonella alonsoi*; (d) *Phakellia robusta*.

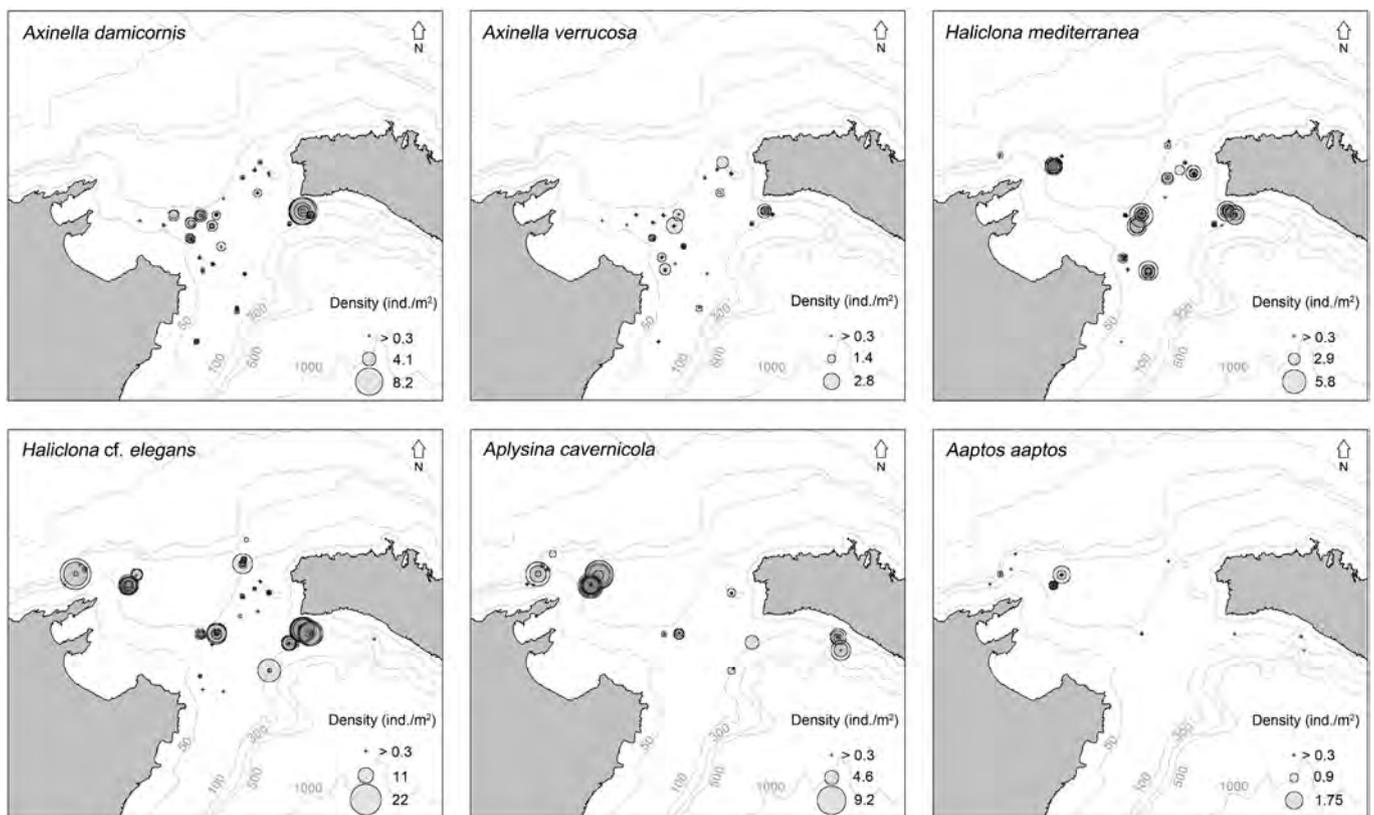


Fig. 7a. Geographical distribution in the study area of the most common species occurring on the continental shelf, represented based on density. Projected view (UTM Zone 31N (WGS84)).

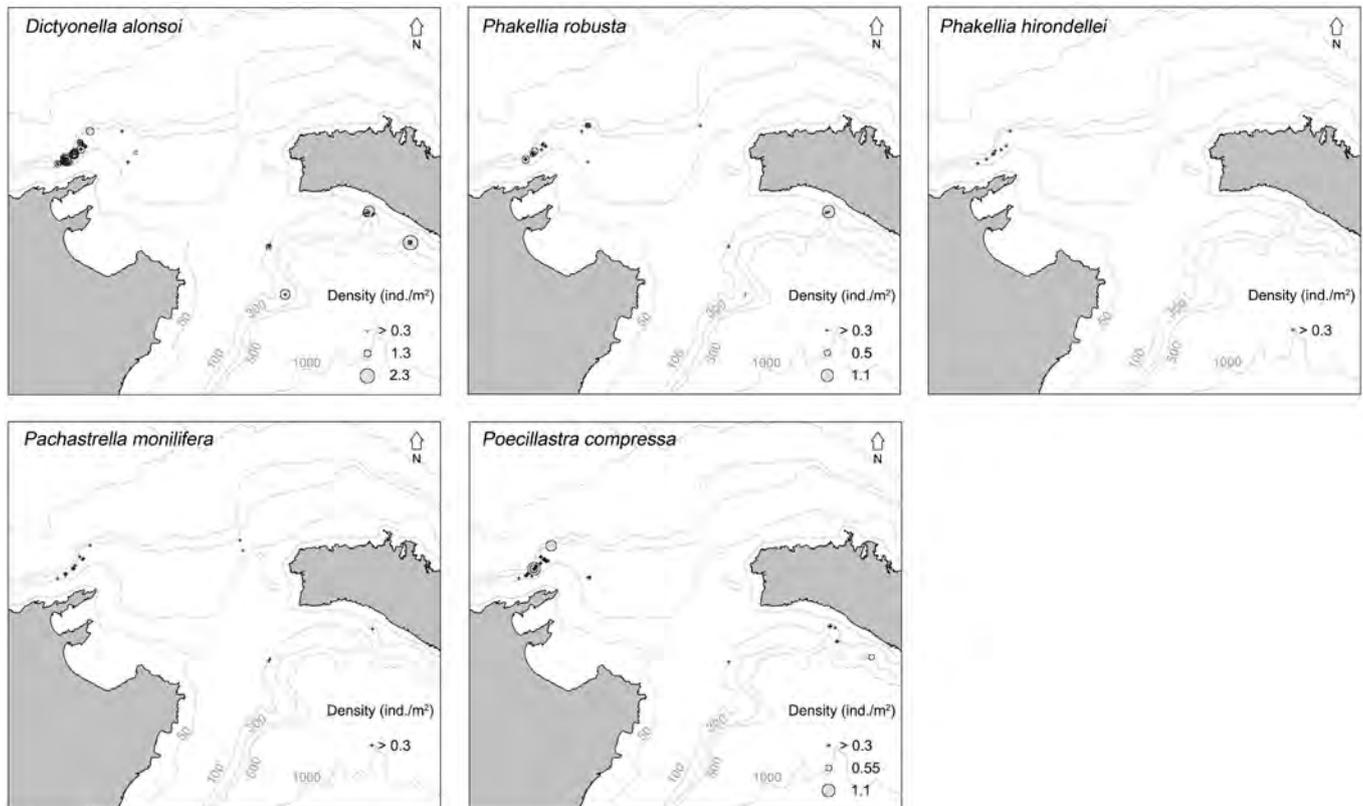


Fig. 7b. Geographical distribution (continuation) in the study area of the most common species occurring on the shelf edge and upper slope, represented based on density. Projected view (UTM Zone 31N (WGS84)).

positively skewed in almost all of their populations, with half of them showing a significant kurtosis.

4. Discussion

A clear bathymetric zonation pattern of sponge species has been observed in the Menorca Channel, with three main groups of species: (i) species inhabiting the inner continental shelf, (ii) species mostly restricted to the outer continental shelf and shelf break and (iii) species with a bathyal affinity, occurring at the shelf edge and the upper slope.

4.1. Inner continental shelf

4.1.1. *Axinella damicornis* and *Axinella verrucosa*

The two target *Axinella* species had a wide distribution in the inner continental shelf, co-occurring in almost all transects (Fig. 3a–c; Table 3). Highest densities were found on horizontal rocky outcrops, but both species could also be found on maërl beds (Fig. 3a–e). These ecological distributions concur with previous records for both *Axinella* species, which are considered characteristic of circalittoral coralligenous communities (Pérès and Picard, 1964) and other dimly lit habitats (Boury-Esnault, 1971; Gerovasileiou and Voultsiadou, 2012). However, despite both axinellids being widely reported from the Mediterranean basin, there is a general absence of quantitative data (abundances) in the bibliography. Density values reported for the Menorca Channel are considerably higher (Figs. 7a; 8a) and comparable with those reported for *Axinella* spp. (1.7 to 7.2 ind./m²) on rocky outcrops of the Tyrrhenian Sea at similar depths (Bertolino et al., 2015). Contrastingly, in trawl-exploitable beds of the Aegean Sea, *Axinella* densities are considerably low (0.4 ind./m²) and were shown to be negatively influenced by trawling events (Kefalas et al., 2003). The Gulf of Sta. Eufemia (Tyrrhenian Sea) is considered to be relatively sheltered from trawl-fishing activities (Bertolino et al., 2015), so the occurrence

of similar *Axinella* densities could imply a low fishing pressure on *Axinella* beds in the Channel, as has been observed for other communities in the area (Grinyó et al., 2018a).

However, *Axinella* densities were not homogenous across the Channel, mostly reflecting the presence of scattered hard substrates outcropping from a prevalent sandy seafloor (Barberá et al., 2012; Druet et al., 2017). In this sense, erect sponges are generally favored by stable substrates and low steady currents (Warwick and Uncles, 1980; Bell and Barnes, 2000c) as previously reported for the Balearic Islands, where *A. damicornis* was shown to be positively correlated with low flow velocities (Ordines et al., 2011). Although most populations were recorded on rocky outcrops, the densest *A. damicornis* population (~8 ind./m²) occurred on a maërl bed close to the southern slope (Fig. 3d–e). Maërl beds in the Menorca Channel are known to be highly unstable, linked to punctual or stable high-velocity flows (Cartigny et al., 2017) able to overturn the maërl matrix (Basso, 1998). As so, the punctual presence of dense *Axinella* fields in such environments may suggest a wider tolerance for substrate instability and flow velocity than previously thought. Finally, *A. damicornis* was more abundant than *A. verrucosa* at most sites (Figs. 7a; 8a), concurring with previous records for both species, where *A. verrucosa* tended to be less abundant than *A. damicornis* (Uriz, 1982; 1983 and references within both). Additionally, *A. damicornis* has been recorded on a wider geographical and bathymetrical distribution, being present in shallow-shaded habitats (Sarà, 1964) and North Atlantic waters (Ackers et al., 1992), where *A. verrucosa* seldomly occurs. Overall, the abundance and distribution of both species allows inferring a more limited dispersal capability (Uriz et al., 1998) and/or a narrower degree of tolerance concerning environmental factors (Wilkinson & Evans, 1989) for *A. verrucosa* compared to *A. damicornis*.

In terms of size-distribution, based on the taxonomic remarks (Siribelli, 1961; Rützler, 1965; Pansini, 1984; Uriz, 1983) populations of both *Axinella* species can be assumed to range between 4 and 7 cm in

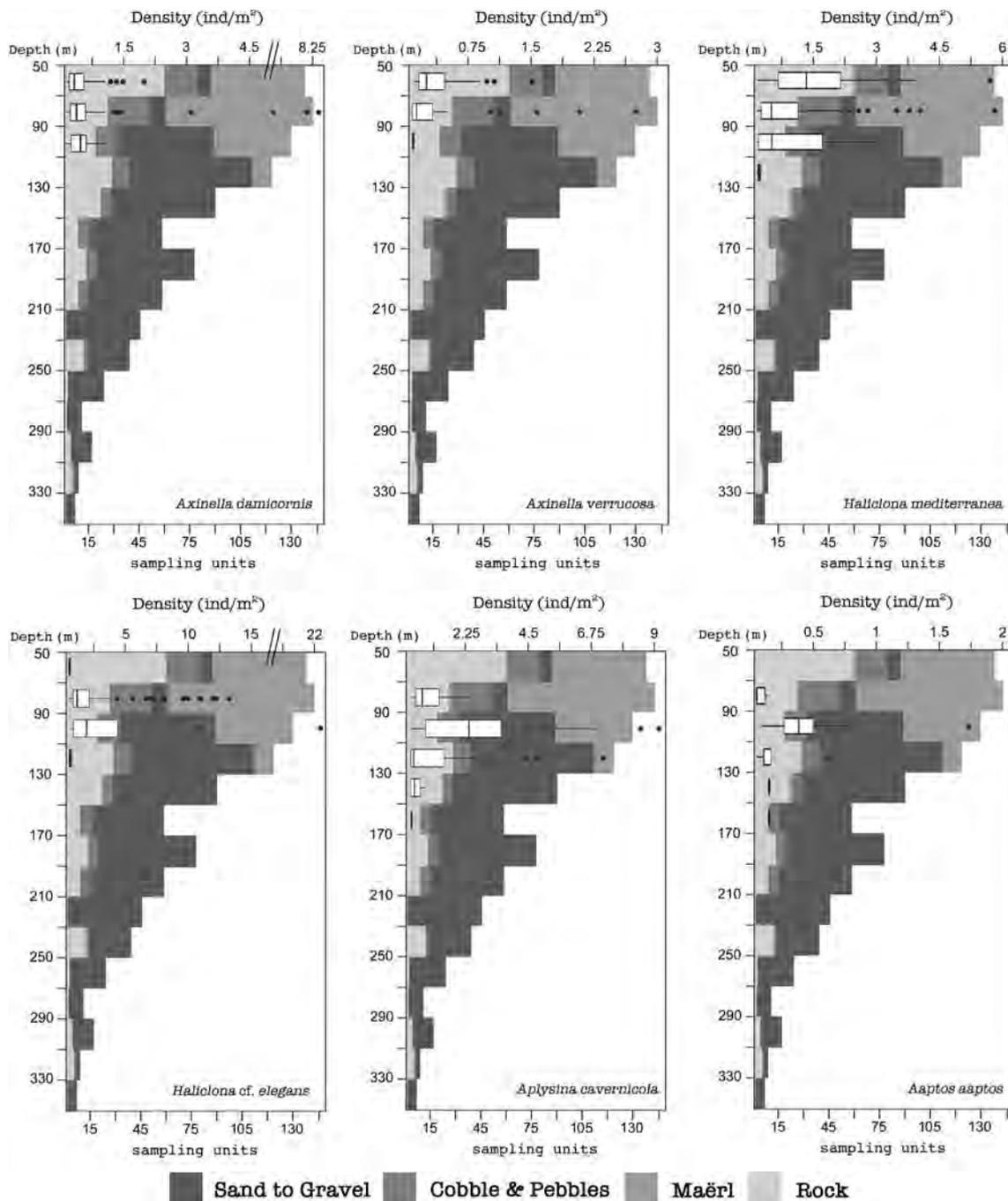


Fig. 8a. Bathymetrical distribution of the most common species occurring on the continental shelf represented along the studied bathymetric range. Boxplots represent the density of a given species at each depth interval. The box’s black line represent the median density value; the squares at each side represent the lower (25%) and upper quartile (75%); the whiskers represent the minimum and maximum values excluding outliers; black dots represent lower and upper outliers, defined as values 3/2 greater or lower than that of the upper and lower quartiles. Gray-scale histograms represent the total number of sampling units for each substrate type (see legend) over the studied bathymetric range.

height, while the maximum height is consistently reported between 8 and 10 cm (e.g. [Topsent, 1934](#); [Uriz, 1983](#)), with some individuals of *A. verrucosa* growing up to 20 cm ([Babić, 1922](#); [Siribelli, 1961](#)). As so, *A. damicornis* and *A. verrucosa* populations in the Menorca Channel concur with previous records, being dominated by small-sized individuals of ~4 cm height, with tails up to 10 cm ([Fig. 9a](#)). Considering that *A. damicornis* is a slow-growing, long-lived species known to undergo growth stagnation for years ([Pansini and Pronzato, 1990](#)), the presence of tails of up to 10 cm might imply these are long-established populations. Furthermore, unimodal size-class distributions with long tail are typical of sessile invertebrates ([Linares et al., 2008](#); [Bo et al., 2012](#)),

while the dominance of small individuals indicates high recruitment success ([Linares et al., 2008](#)). In this regard, it must be noted that almost all populations had a large proportion of small, yellow-ochrish recruits that, due to their aberrant or undifferentiated morphology ([Sarà, 1964](#)), could not be assigned to a given species ([Fig. 3a–c](#)). This high proportion of small individuals could derive from recruitment pulses, as observed in other areas ([Dayton et al., 2016](#)). Furthermore, rocky substrates, seasonal algal growth ([Baldacconi and Corriero, 2009](#)), competition with other benthic organisms ([Jackson and Buss, 1975](#); [Pansini and Pronzato, 1990](#); [Bell and Barnes, 2003](#)) and predation ([Haber et al., 2011](#)) might regulate recruitment success, growth

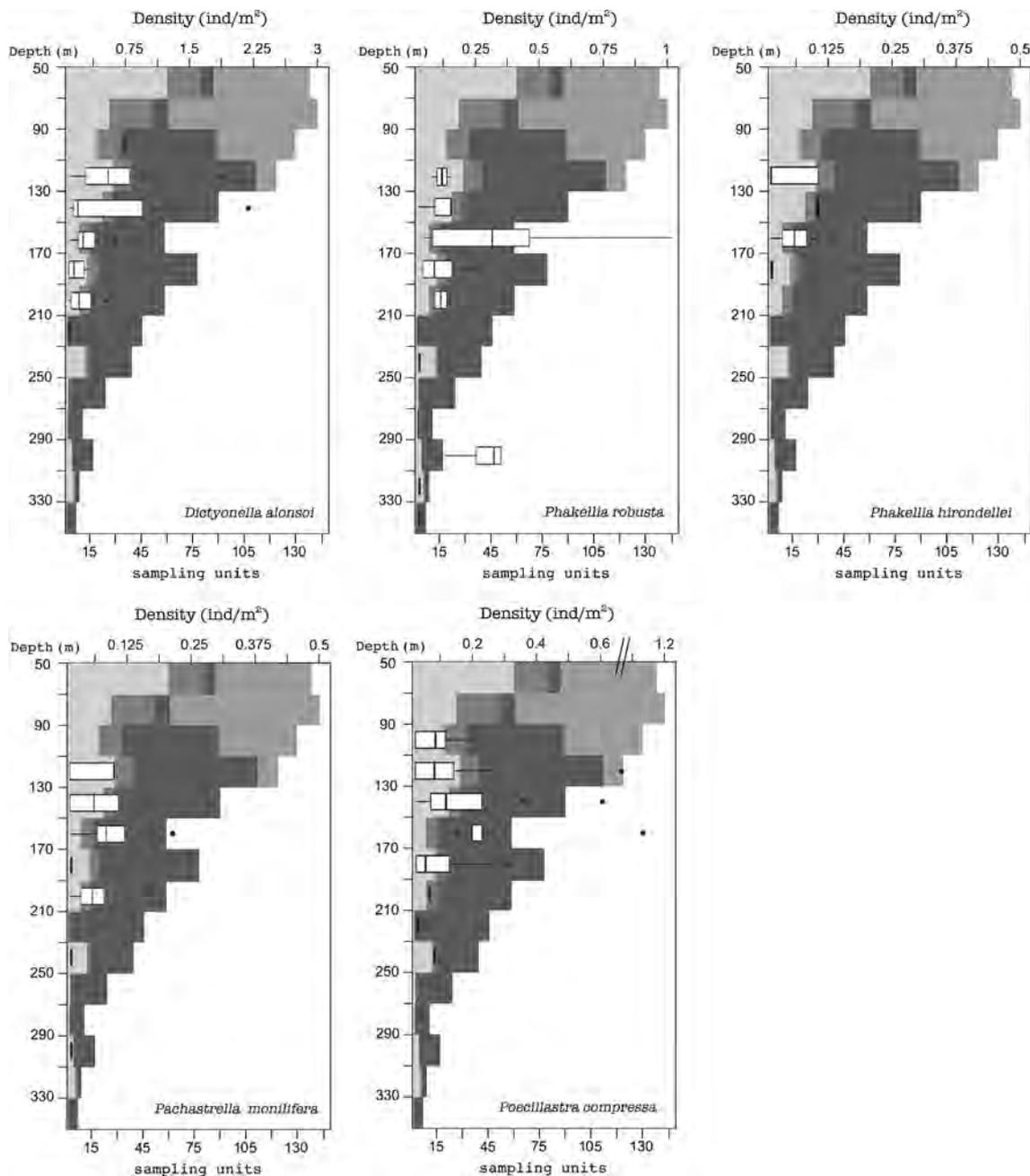


Fig. 8b. (Continuation) Bathymetrical distribution of the most common species occurring on the shelf edge and upper slope along the studied bathymetric range. Boxplots represent the density of a given species at each depth interval. Gray-scale histograms represent the total number of sampling units for each substrate type (see legend in Fig. 8a) over the studied bathymetric range.

and survival, resulting in positively skewed populations.

Finally, correlation between height and width differed for each transect, implying the presence of different growth dynamics or morphologies among the studied sites and the analyzed *Axinella* species. In this regard, sponges are known to be morphologically adaptable to environmental stressors (Palumbi, 1984). As an example, Abraham (2001) found that *Raspailia (Raspaxilla) inaequalis* (planar arborescent sponge) was able to alter its fractal dimension in response to water flux, while Kaandorp and Kübler (2001) demonstrated that *Haliclona (Haliclona) oculata* (lamellated-branching arborescent sponge) could alter its branch morphology in relation to water exposure, with plate-like branches being linked to exposed areas, and thin branches to sheltered ones. In this sense, *A. damicornis* (flattened branches) and *A. verrucosa* (tubular branches) different growth dynamics could respond to site-specific adaptations to environmental constraints (Meroz-Fine, 2005),

as highlighted by both species plastic morphology, being able to develop into a wide array of intermediate morphologies derived from their typical growth forms (Pansini, 1984).

4.1.2. *Haliclona mediterranea*

Maërl beds of the Menorca Channel represent a local diversity hotspot for sessile invertebrates, where sponges are the dominant benthic suspension feeders, both in terms of diversity and abundance (Grinyó et al., 2018a; Santín et al., 2018). Among the targeted species, only *H. mediterranea* occurred in high abundances on the maërl beds of the inner shelf of the Menorca Channel (Fig. 4a), this being the only known location where this species has been observed massively growing on this type of substrates. In the northern Adriatic the species has been reported to rapidly colonize artificial substrates (32 months time-lapse), rapidly achieving high coverage and biomass values (Molin

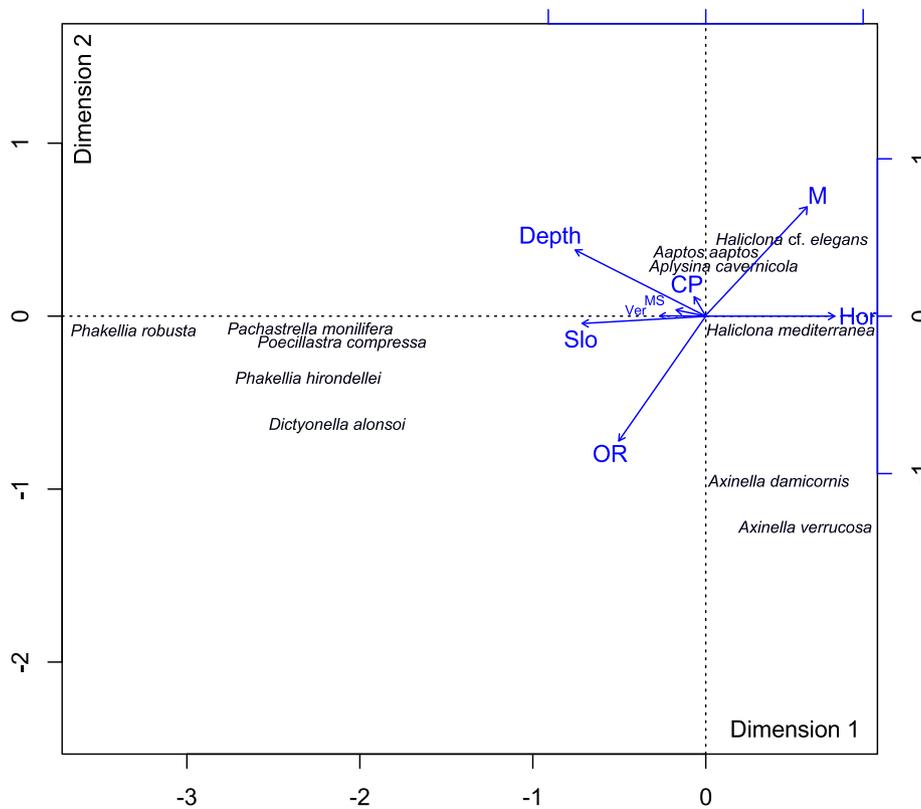


Fig. 9. Canonical correspondence analysis (CCA) biplot showing the ordination of the studied sponge species and the role of the significant environmental variables. M: Maërl; OR: Rocky outcrops; CP: Cobbles and Pebbles MS: Medium Sands; Hor: Horizontal; Slo: Sloping; Ver: Vertical.

Table 2

Sponge morphometry. Ratio between height, width/diameter and perimeter for each studied species. Equations calculated based on a linear regression. N refers to the total number of individuals of each species used for the calculations.

| Species | N | Height vs. Width | | Height vs. Perimeter | | Width vs. Perimeter | |
|--------------------------------|------|----------------------|----------------|-----------------------|----------------|----------------------|----------------|
| | | Equation | R ² | Equation | R ² | Equation | R ² |
| <i>Axinella damicornis</i> | 1558 | y = 0.7856x + 0.221 | 0.5995 | – | – | – | – |
| <i>Axinella verrucosa</i> | 807 | y = 0.8424x – 0.2818 | 0.6504 | – | – | – | – |
| <i>Aaptos aaptos</i> | 177 | y = 1.1986x + 0.3498 | 0.3747 | y = 0.1442x + 1.5893 | 0.53357 | y = 2.498x + 2.3789 | 0.93209 |
| <i>Pachastrella monilifera</i> | 83 | y = 1.6519x – 1.561 | 0.68046 | y = 0.1668x + 2.0469 | 0.78673 | y = 2.6062 + 3.3079 | 0.9629 |
| <i>Phakellia hironellei</i> | 36 | y = 1.4136x + 1.0824 | 0.70098 | y = 0.19558x + 1.8717 | 0.81904 | y = 2.6719x + 3.5767 | 0.87984 |
| <i>Phakellia robusta</i> | 257 | y = 1.4136x + 1.0824 | 0.70098 | y = 0.19558x + 1.8717 | 0.81904 | y = 2.6719x + 3.5767 | 0.95303 |
| <i>Poecillastra compressa</i> | 405 | y = 1.275x + 2.2421 | 0.45154 | y = 0.1597x + 1.8429 | 0.63633 | y = 2.5271x + 4.2467 | 0.92153 |

Table 3

Size structure characteristics of the studied species based on selected transects (the complete table can be found at the supplementary material 2). Morphometric parameters include: height, width, perimeter (when applicable), standard deviation (SD), skewness and kurtosis. Significance levels for skewness and kurtosis are represented as follows: * (p-value < 0.05) ** (p-value < 0.01) *** (p-value < 0.001). The complete table can be found at the supplementary material.

| Species | Transect | Individuals (n) | Height (cm) | | Width/ Diameter (cm) | | Perimeter (cm) | | Skewness | Kurtosis |
|----------------------|----------|-----------------|-------------|-------|----------------------|-------|----------------|--------|----------|-----------|
| | | | Mean | SD | Mean | SD | Mean | SD | | |
| | | | Max. | Max. | Max. | Max. | Max. | Max. | | |
| <i>A. damicornis</i> | 60 | 267 | 2.81 ± 1.58 | 8.78 | 2.34 ± 1.71 | 9.14 | – | – | 1*** | 3.95* |
| | 71 | 468 | 3 ± 1.62 | 10.1 | 1.97 ± 1.25 | 6.33 | – | – | 0.913*** | 3.9** |
| <i>A. verrucosa</i> | 55 | 118 | 2.59 ± 1.14 | 6.01 | 2.47 ± 1.42 | 6.54 | – | – | 0.603** | 3.118 |
| | 60 | 275 | 3.17 ± 1.69 | 9.61 | 1.97 ± 1.39 | 7.02 | – | – | 0.846*** | 3.58 |
| <i>A. aaptos</i> | 6 | 68 | 4.25 ± 1.62 | 8.6 | 5.16 ± 2.33 | 12.88 | 15.9 ± 6.67 | 37.59 | 0.928*** | 3.822 |
| | 24 | 40 | 3.04 ± 1.33 | 5.5 | 3.73 ± 1.7 | 10.01 | 11.16 ± 5.17 | 29.28 | 2.802*** | 6.002*** |
| <i>D. alonsoi</i> | 7 | 65 | 4.44 ± 1.85 | 9.97 | – | – | – | – | 0.571 | 3.392 |
| | 77 | 53 | 2.8 ± 1.19 | 6.33 | – | – | – | – | 0.83* | 3.220 |
| <i>P. robusta</i> | 6 | 37 | 10.19 ± 5 | 29.25 | 15.62 ± 11.1 | 67.19 | 45.69 ± 28.41 | 174.96 | 2.899*** | 13.837*** |
| | 81 | 61 | 5.47 ± 3.14 | 13.81 | 5.97 ± 5.15 | 15.05 | 18.64 ± 11.87 | 51.82 | 0.471 | 2.002 |
| <i>P. compressa</i> | 6 | 94 | 6.55 ± 3.76 | 20.51 | 10.99 ± 6.57 | 31.73 | 31.48 ± 17.11 | 79.22 | 0.693*** | 3.136 |
| | 7 | 45 | 10.3 ± 5.27 | 20.84 | 15.74 ± 8.39 | 45.86 | 45.45 ± 21.53 | 105.95 | 1.166*** | 5.103** |

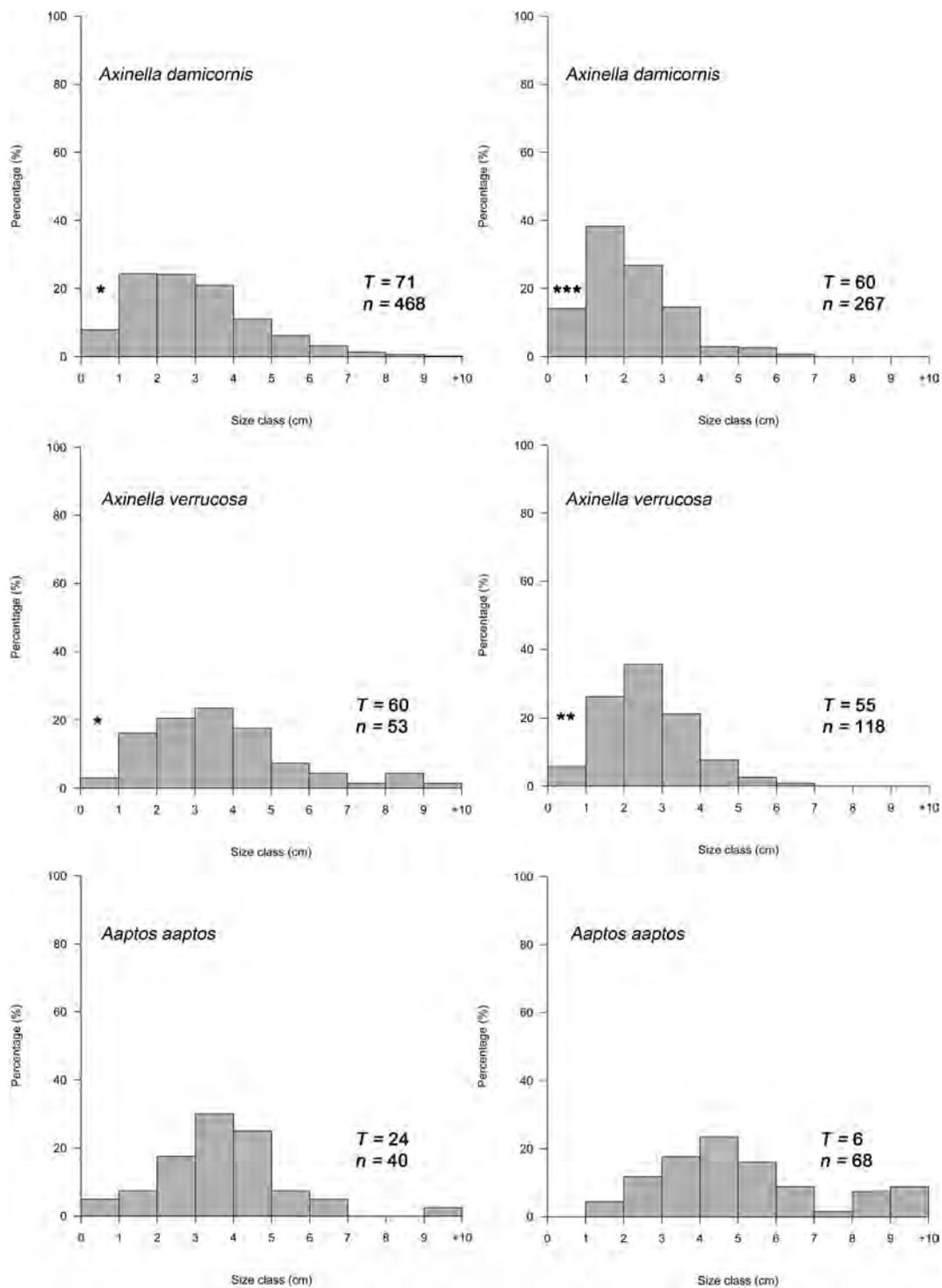


Fig. 10a. Size-structure distribution for *A. damicornis*, *A. verrucosa* and *A. aaptos* based on the selected transects in Table 3. Transect's (T) number as in Fig. 1, number of individuals (n) as in Table 3. Asterisks indicate the presence of recruits as: * scarce; ** abundant; *** very abundant.

et al., 2008), comparable with those of typical opportunistic or pioneering taxa such as hydrozoans (Gili and Hughes, 1995). Furthermore, in the Trieste Bay, *H. mediterranea* has been reported to colonize bare rocks in less than one year after the first coralline algae were observed (Piron et al., 2007). Withal, the dominance of *H. mediterranea* in maërl beds was restricted to a small depth window (50–70 m depth), being replaced by *H. cf. elegans* as depth increased. This depth window is subjected to higher temperatures (over 15 °C all year) than other Mediterranean areas at similar depths, with peaks of 21 °C in autumn (Ballesteros and Zabala, 1993). High temperatures have been identified

to have a strong influence in the seasonality of benthic suspension feeders, with several species observed to undergo aestivation or winter dormancy processes (Coma et al., 2000). *Haliclona mediterranea* individuals overgrowing *Corallium rubrum* colonies have been observed to appear and then disappear in a few months period (FAO, 1984), while in the Medes Islands its presence also fluctuates drastically at a yearly scale, which has been likely attributed to temperature changes (Gómez-Gras pers. comm.). This ability to colonize new substrates, paired with its capacity to persist in unstable substrates such as maërl beds infers that *H. mediterranea* behaves, under certain environmental conditions,

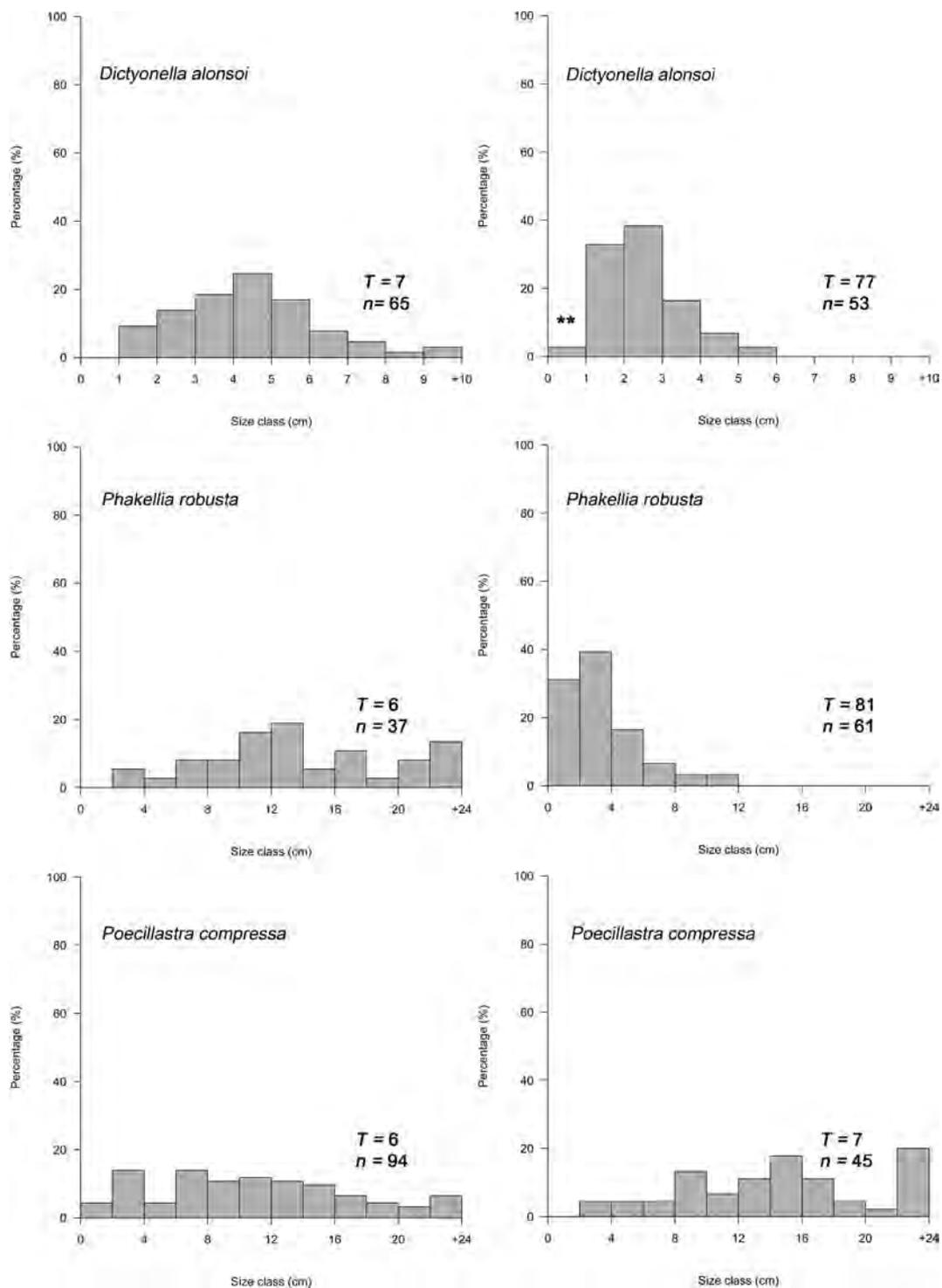


Fig. 10b. Size-structure distribution (continuation) for *D. alonsoi*, *P. robusta* and *P. compressa* based on the selected transects in Table 2. Transect's (T) number as in Fig. 1, number of individuals (n) as in Table 3. Asterisks indicate the presence of recruits as: * scarce; ** abundant; *** very abundant.

as an opportunistic species, which might explain its sole domination and abundance in the Channel's inner maërl beds.

4.2. Outer continental shelf

4.2.1. *Haliclona cf. elegans*, *Aplysina cavernicola* and *aaptos aaptos*

Haliclona cf. elegans and *A. cavernicola* were mostly distributed at the northern and southern outer continental shelf limits, being always found on maërl beds and coralligenous concretions (Fig. 4b–e) over large continuous extensions. *Aaptos aaptos* occurred within both species

dense fields (Fig. 4c–d; f), yet it was scarcer and spatially spaced. Despite concentrating towards the outer shelf, several less-dense patches of *H. cf. elegans* could still be found on the inner shelf, while *A. cavernicola* and *A. aaptos* were punctually observed in crevices and shaded hard substrates (Wilkinson and Vacelet, 1979). The presence of individuals, even at low frequencies may play a paramount role in terms of connectivity between populations occurring across the Channel's area. Northern and southern sponge populations are separated by extensive sandy areas (Druet et al., 2017), which may act as a physical barrier for hard-bottom sponges' dispersal (van Soest, 1993). Thus,

while being irrelevant in terms of abundance and biomass when compared to the outer shelf area, these isolated sponge patches might act as stepping-stones, connecting northern, southern and littoral populations, maintaining the genetic flux between populations, as theorized for other species (Collette and Rützler, 1977; Wörheide et al., 2008). Whilst all three evaluated sponges shared a common distribution pattern in the northern area of the Channel, notable differences occurred at the southern limit of the outer continental shelf, where overall lower densities were recorded (Fig. 7a). The observed trend could partially reflect the differences of the main water bodies affecting each side of the Channel, with southern areas receiving a more oligotrophic, intermittent water flow compared to northern ones (García et al., 2005).

The vast, dense fields of *A. cavernicola* in the north might be a remarkable feature of the study area (Fig. 4b), as sponge densities are comparable to those known to occur in low-impacted areas of the Mediterranean (Bertolino et al., 2015). The species life span is unknown, but the monitoring of a population in littoral environments during 5 years showed less than 15% mortality over the course of the study (Teixidó et al., 2006). Additionally, sexual reproduction rates of *Aplysina* spp. highly diminishes with depth (Maldonado and Young, 1998), being considered almost non-existent at the depth range (~70–180 m) where it occurs in the Menorca Channel (Teixidó et al., 2006). Finally, the Channel's maërl beds have undergone illegal bottom trawling during the past years (García et al., 2014), which could have seriously affected *A. cavernicola* populations, as dredging has been shown to have dramatic effects on the abundance of *Aplysina* species in the Aegean Sea (Kefalas et al., 2003; Gerovasileiou et al., 2018). Considering the slow-growth and low-recruitment shown by the species (Maldonado and Young, 1998; Teixidó et al., 2006), paired with its unusually high densities at the study area, it can be assumed that the *Aplysina* fields here recorded have remained unaltered for a long time.

Although size-frequency could not be evaluated for *H. cf. elegans* and *A. cavernicola*, *A. aaptos* showed a consistent globular shape as in other deep-water habitats (Vidal, 1967; Uriz, 1983) allowing for comparisons to be made. The only size-distribution data for *A. aaptos* comes from coralligenous formations in Torrielles, France (Vidal, 1967), where the species is reported as very abundant, with a mean diameter between 4 and 6 cm, concurring with the average diameter values observed in the Menorca Channel (Table 3; Supplementary material 2). However, widest records observed (20–30 cm in diameter), most likely resulting from the fusion of individuals from asexual reproduction (Fig. 4c–d; f), were far above most records of the species (e.g. Babić, 1922; Uriz, 1983 and references therein). The live span of sponge species is known to increase with depth (Montero-Serra et al., 2018), so these unusual high dimensions could strengthen the view that the Menorca Channel sponge grounds have not been severely impacted by bottom trawl practices, as has occurred in other Mediterranean areas (Gerovasileiou et al., 2018).

4.3. Shelf edge and upper slope

4.3.1. Lamellate sponges and *Dictyonella alonsoi*

Pachastrella monilifera, *Poecillastra compressa*, *Phakellia robusta* and *Phakellia hirondelei* showed a clear bathyal affinity, occurring almost exclusively at shelf break and slope areas (110–170 m depth) on sloping to vertical rocky outcrops (Figs. 5e–g, 9). Lamellate sponges are considered common inhabitants of cold and deep waters along the Atlanto-Mediterranean region (Vacelet, 1969; Bo et al., 2012; Sitjá and Maldonado, 2014), with *P. compressa* and *P. monilifera* being considered its main constituents (Maldonado et al., 2015). In contrast, in the Menorca Channel, the most abundant lamellate sponges were *P. compressa* and *P. robusta*, as it has been reported for the Mediterranean French coast (Fourt et al., 2017). Furthermore, recent works in the Alboran Sea found that lamellate sponges occurred not just at the shelf edge's rocky bottoms, but also on shallow maërl beds, at 60–80 m depth (Sitjá and Maldonado, 2014), whereas in the Menorca Channel their presence in

maërl beds was residual, with just a few scattered *P. compressa* individuals present (90–110 m depth). In the Channel, lamellate sponges concentrated towards Cap Formentor (northern slope), and the Menorca Canyon (southern slope), which are among the most active areas in terms of water flow in the Channel (Acosta et al., 2003; Amores and Montserrat, 2014). These findings strengthen the linkage between lamellate sponges and water currents, as it has been observed in other Mediterranean areas (Bo et al., 2012). To summarize, Mediterranean lamellate sponge assemblages seem to occur in a wide range of environmental conditions, however its distribution and composition appears to be constrained by species-specific habitat requirements, as it has been demonstrated for other deep benthic fauna (Buhl-Mortensen et al., 2015).

Most *P. robusta* and *P. compressa* populations were generally dominated by medium-sized individuals, in accordance with lamellate sponge populations (*P. compressa* and *P. monilifera*) alongside the Pugliese area (Bo et al., 2012). Additionally, all but one *P. robusta* populations (Table 3; Supplementary material 2) fell within the “large-sized sponge” category (> 5 cm) for Atlantic waters (OSPAR, 2010), yet with just one above the “adult size” category (> 10 cm). The single small-size dominated *P. robusta* population could respond to reproduction pulses, as observed for other cold-water sponges (Dayton et al., 2016), which are considered a major driver for sponge population increase (McMurray et al., 2010). Furthermore, the observed lamellate sponges are commonly reported as accompanying species of *Dendrophyllia* spp. (Vacelet, 1969; Rodríguez-Solorzano and Durán, 1982) and reef building cold-water corals (Vacelet, 1969; Bo et al., 2012) at shelf edge and slope environments. However, *Dendrophyllia* and cold-water corals are fairly scarce in areas shallower than 200 m depth in the Menorca Channel (Gori et al., 2017), leaving lamellate sponges as one of the main ecosystem engineers between 140 and 230 m depth, alongside with gorgonians and antipatharians (Grinyó et al., 2016).

Alongside lamellate sponges and gorgonians, we found dense aggregations of *Dictyonella alonsoi* (Fig. 5a; j; i), a species previously known from 3 individuals found in a cave in the Alboran Sea (Carballo et al., 1996). The finding of shared sponge species between deep-sea and caves environments has become frequent thanks to the use of ROVs and manned-submersibles (Bakran-Petricioli, et al., 2007) and highlights the connection between these two environments (Harmelin and Vacelet, 1997). The co-occurrence of small erect sponges alongside lamellate ones is a common trait (Cabioch, 1961; Sitjá and Maldonado, 2014), as the former benefits from the turbidity created by the larger sponges (Bo et al., 2012), reinforcing the view that lamellate sponges may play a role as engineering species in the same way of anthozoans in deep environments (Bo et al., 2012; Maldonado et al., 2015).

In terms of size-distribution, *D. alonsoi* populations followed a similar pattern to that of *A. damicornis* and *A. verrucosa*, with populations dominated by small-medium individuals around 3 cm height and a vast presence of small recruits (Fig. 5d). *Dictyonella alonsoi* is the only species occurring in the shelf edge and the upper slope not associated with vertical substrates, mostly occurring on sloping and horizontal ones (Fig. 9) (Santín et al., 2018). Since *D. alonsoi* seemingly occurs in active hydrodynamic settings (Acosta et al., 2003; Iacono, et al., 2014) but is almost absent in vertical substrates, its distribution, abundance and size-structure could be limited to a certain extent by the combined effects of water currents, sedimentary processes and/or substrate inclination, which are known to potentially limit the distribution of sponges (Bell and Barnes, 2000a; 2000b).

4.4. General trends of the studied species

Depth and substrate type were the main factors explaining sponge distribution in the Menorca Channel (Fig. 9), yet the influence of substrate type was mostly restricted to the continental shelf, where higher heterogeneity occurs (Druet et al., 2017). Preference for sloping surfaces was intimately related with depth (Fig. 9a and b) yet, in contrast,

the morphological strategies of the studied sponges species did not vary with it, but were mostly associated with specific substrate types.

Erect, arborescent and lamellate sponges were mostly linked to rocky outcrops, regardless of depth, yet the biggest forms were restricted to the deepest part of the studied area. These findings concurs with records for other sessile benthic organisms, as arborescent forms are favored by stable substrates (Ordines et al., 2011), while at the same time bigger individuals are restricted to deeper areas due to a more stable hydrodynamic flux (Gili et al., 1989). Species with a more encrusting or reptant (e.g. *H. mediterranea* and *A. cavernicola*) morphology proliferated on maërl beds on the continental shelf. Inner maërl beds were almost exclusively colonized by *H. mediterranea*, which exhibited opportunistic strategy traits, a characteristic of organisms living on unstable environments (Gili et al., 1989). On the contrary, the outer maërl beds were an amalgam of species of diverse morphologies, including chimney-like (*H. cf. elegans*), tubular (*A. cavernicola*) or massive-globular (*A. aaptos*) shapes. This might reflect the presence of different microhabitats and/or major consolidation of the outer maërl beds (Pereira-Filho et al., 2015), favoring the presence of diverse and contrasting growth morphologies (Jackson and Buss, 1975; Longo et al., 2018).

Nevertheless, other parameters not considered in this study (e.g. water transparency, suspended particles, hydrodynamics or temperature) might also play a major role in species distribution (Magalhães et al., 2015), resulting in predominant and, consequently, morphologically better adapted species for each substrate type and set of environmental conditions in the area.

5. Conclusions

Overall, the studied sponges presented a large distribution among the continental shelf area, with several dense, reproductive populations occurring in a wide range of hard substrates. Sponge grounds are currently listed as Vulnerable Marine Ecosystems (VMEs) by the FAO (2009), and appear as threatened habitats under the OSPAR commission, 2010. As the Menorca Channel is soon to be declared an MPA, this study provides a reliable baseline for future monitoring of the most abundant and structuring sponges dwelling in the area. Finally, in a context of global change, we would like to highlight the existing knowledge gap regarding the demographic patterns, biotic and abiotic factors affecting their distribution, their role in Mediterranean benthic communities and the need for generating reliable and replicable demographic data for sponges, in order to be able to monitor changes over time.

Acknowledgments

The authors thank the crews of the R/V García del Cid, Miguel Oliver and SOCIB, the JAGO team (J. Schauer and K. Hissmann) from IFM-GEOMAR (Kiel, Germany), the NEMO ROV pilot Gavin Newman and David Díaz for their help during oceanographic surveys, Eneko Aspillaga for their help with spatial data treatment, and David Díaz, Creu Palacín and Carlota Ruiz for their aid. 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) and the EU-ENPI CBC-Med project ECOSAFIMED ENPI-ECOSAFIMED-II-B/2.1/1073 (“Towards Ecosystem Conservation and Sustainable Artisanal Fisheries in the Mediterranean basin”) (2014–15).

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocan.2019.02.002>.

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