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Soft corals assemblages in deep environments of the Menorca Channel (Western Mediterranean Sea)

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ABSTRACT

Image-based research in mesophotic and deep environments of the Mediterranean Sea has significantly increased during the past decades. So far, this research has been focused on the ecology of key structuring organisms such as scleractinians, antipatharians, gorgonians or large demosponges. However, the ecology of true soft corals has barely been studied and is still in a very preliminary stage. To overcome this situation, soft coral assemblages in shelf and slope environments of the Menorca Channel (Western Mediterranean Sea) have been studied through the quantitative analysis of 85 video transect recorded over 38500 m^2. Highest soft coral diversity was encountered on the shelf edge, resembling deep Mediterranean gorgonian patterns. Three soft coral assemblages, segregated by depth, substrate, and slope were identified: two monospecific ones composed by *Nidalia studeri* and *Alcyonium palmatum*, respectively and a multispecific one composed by *Paralcyonium spinulosum*, *Alcyonium* sp., *Chironephthya mediterranea* and *Daniela koreni*. The evaluated species presented average densities within the same range as other deep Mediterranean anthozoans ranging from 1 to 9 col.$\cdot m^{-2}$. However, *N. studeri* and *P. spinulosum* punctually formed dense monospecific aggregations, reaching maximum densities of 49 col.$\cdot m^{-2}$ and 60 col.$\cdot m^{-2}$ respectively. Both species monopolized vast extensions of the continental shelf and shelf edge. The identification and ecological characterization of these assemblages brings new insight about deep Mediterranean anthozoan communities, and provides baseline for future management plans in the study area.

1. Introduction

Cold water corals (CWC) are extremely diverse including a wide range of anthozoans such as hydrocorals, scleractinians, antipatharians, gorgonians, or soft corals among others (Roberts et al., 2009). In deep environments worldwide, CWC are among the main structural species (e.g. Mortensen and Buhl-Mortensen, 2004; De Clippele et al., 2019), providing a three-dimensional structure that increases spatial heterogeneity and provides refuge to a variety of associated species (Buhl-Mortensen and Mortensen, 2005; Roberts et al., 2009; D'Onghia, 2019). During the past decades, research focused on these organisms has substantially increased worldwide due to the use of telepresence technologies, such as remotely operated vehicles (ROVs) or autonomous underwater vehicles (AUV) (Hall-Spencer et al., 2002; Gori et al., 2013; Baco et al., 2017). In the Mediterranean Sea, the discovery of several CWC habitats during the 1990's (e.g. Tursi et al. 2004; Schembri et al., 2007; Etiope et al., 2010) triggered an ongoing image-based research on the ecology of key structuring organisms. So far, this research has been focused on, framework-building scleractinians (Orejas et al., 2009; Gori et al., 2013; Chimienti et al., 2018a, 2019; Corbera et al., 2019), gorgonians (Bo et al., 2012; Grinyó et al., 2016), bamboo-corals (Mastrototaro et al., 2017; Bo et al., 2020), antipatharians (Bo et al., 2009, 2014, 2015; Deidun et al., 2014; Massi et al., 2018) and demosponges (Bertolino et al., 2015; Santín et al., 2018, 2019). Contrastingly, true soft corals, understood as a subgroup of alcyonaceans characterized by fleshy soft-bodied colonies without a supporting skeletal axis and with a non-encrusting morphology (Octocorallia: Alcyonacea: Alcyoniina; Lumsden et al., 2009), have remained understudied. Research regarding this group in deep areas of the Mediterranean Sea has mostly been focused on taxonomic aspects (López-González et al.,

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2012, 2015). In this regard, approximately eight soft corals species have been identified in deep environments of the Mediterranean Sea (Aguilar et al., 2017), some of them being recently described to science such as *Chironephthya mediterranea* (López-González et al., 2015) or rediscovered such as *Nidalia studeri* (Koch, 1891) (see López-González et al., 2012) or *Daniela koreni* von Koch, 1891 (López-González, unpublished data). Additionally, other cryptic species within the genus *Alcyonium* are still being discussed and yet to be resolved throughout molecular analyses and morphological descriptions (López-González, unpublished data).

During the past decades Mediterranean continental shelves and slopes have been chronically impacted by bottom trawling, longline fishing and to a lesser extent artisanal fishing which is generally constrained to littoral and inner shelf environments (Smith et al., 2000; Maynou and Cartes, 2012; Mytilineou et al., 2014; Purroy et al., 2014; Bo et al., 2015; Enrichetti et al., 2019a). These fishing practices cause direct impacts on vulnerable marine ecosystems (VME) by removing, damaging or entangling habitat-forming species (Maynou and Cartes, 2012; Mytilineou et al., 2014; Enrichetti et al., 2019a). Due to their erected branching morphology, soft structure, low growth rates and high longevities, soft corals are extremely susceptible to these physical disturbances (Cordes et al., 2001); and can represent a large proportion of fishing bycatch in Mediterranean fisheries (Voultsiadou et al, 2011; Petović et al., 2016). In order to preserve areas that are still relatively well structured, the European Union has engaged in the establishment of special areas of conservation (SAC) for the Natura 2000 network. The Menorca Channel, hosts important benthic habitats and communities worthy of protecting, according to the EU Habitat Directive (Grinyó et al., 2018). Consequently, this area has recently been declared a site of community interest (SCI) within the Nature 2000 network and is currently awaiting the development and application of a spatial management plan. For this reason, an exhaustive image-based exploration of mesophotic and deep benthic environments of the Menorca Channel was recently made, revealing the presence of well-preserved VME that occur over wide extents of the continental shelf and slope (Grinyó et al., 2016, 2018; Santín et al., 2018, 2019). In some of these assemblages, soft corals reached high abundances, representing the main habitat forming species (Grinyó et al., 2018). However, these studies have only proportioned a brief glimpse of this group's ecology and large knowledge gaps still remain.

In this context, we hypothesize that a) the Channel hosts different soft coral assemblages that b) respond to different environmental parameters, and that c) soft coral diversity is unevenly distributed within the explored geographic and bathymetric range. To answer these hypotheses this study has characterized the diversity and abundance of soft coral in mesophotic and deep habitats over a large bathymetrical extent (∼40–360 m depth); assessing their vertical and geographic distribution patterns; and gain insight into some of the environmental drivers influencing their occurrence.

2. Material and methods

2.1. Study area

The Menorca Channel is located in the Western Mediterranean Sea (39°53′0.73″N, 3°29′51.16″E) between the islands of Mallorca and Menorca (Fig. 1). The Channel's shelf (40–100 m depth) extends between both islands covering an approximate area of 2000 km^2 and is widely covered by maërl beds and soft sediments, with hard substrates restrained to scattered coralligenous outcrops (Druet et al., 2017). The shelf edge (100–180 m depth) and continental slope (180–340 m depth) are characterized by smooth reliefs covered by large extensions of detritic sediments, while hard substrates where mostly constrained to the proximities of Cap Formentor and in the Menorca Canyon head (Fig. 1A and B) where vertical rocky walls are the dominant substrates (Grinyó et al., 2016). Hydrologically, the Menorca Channel is located in a boundary zone between the Balearic and the Algerian sub-basins. The northern shelf edge and continental slope is influenced by the Balearic Current (Balbín et al., 2012) and its associated front (Ruiz et al., 2009), that flow northward over the continental slope of the Balearic archipelago at approximately 200 m depth (Ruiz et al., 2009). Except for the Menorca Canyon, where daily tidal currents occur (Grinyó et al., 2017), there are no constant currents influencing the southern slope of the Channel. This area is influenced by the sporadic arrival of mesoscale structures coming from the Algerian Current and the Almeria-Oran front (García et al., 2005).

2.2. Video recording

A total of 85 video transects were recorded during seven different surveys in the frame of the LIFE + INDEMARES, ENPI-ECOSAFIMED and LIROBAL projects on board of the R/V "García del Cid" (September 2010, April 2011, October 2011, June 2012), the R/V "Miguel Oliver" (August 2011), the R/V SOCIB (July 2014) and the R/V Ángeles Alvariño (May 2015). From these surveys, 20 video transects were recorded with the manned submersible JAGO (IFM-GEOMAR), 65 video transects were recorded with the ROV "NEMO" (Gavin Newman) and one video transect was recorded with the ROV "LIROPUS" (Instituto Español de Oceanografia). Video transects covered an area of 38,500 m^2 recorded over linear distance of 77.5 km and a width of 0.5 m. The JAGO and both ROVs were equipped with a high definition camera, a grabber and two parallel laser beams (50 cm for the Jago and 10 cm for the NEMO and LIROPUS ROVs) that provided a scale used to define a fixed width of the transects during the following video analysis. Transects were recorded in a close-zoom (∼0.5–1.5 m width of view) and in a digital format. Positioning of JAGO, NEMO and LIROPUS was achieved with underwater acoustic positioning systems. All instruments moved at an approximate constant speed of 0.3 knots and transect lengths ranged between 80 and 3000 m, over depths ranging from 45 to 347 m. Transects were randomly located in order to cover the whole study area, however areas that presented morphological features associated to the presence of rocky bottoms were explored more intensively (Fig. 1).

2.3. Video analysis

Quantitative video analysis followed the methodology described in Gori et al. (2011), using the software Final Cut Pro 7 (Apple Inc.). Pauses and loops were removed from the footage to avoid overestimation of transect length. Sequences with poor image quality or recorded too far above the seafloor were discarded from the analysis. After removal of unsuitable sequences, the remaining 93% was considered suitable corresponding to a surface of 36,000 m^2 and a linear distance of 72 km. Every soft coral colony observed within a width of 0.5 m (based on the laser beams) along each video transect was branded with a time reference, resulting from the time elapsed since the beginning of the video transect to the crossing of the laser beams with the base of the colony (Gori et al., 2011). A similar procedure was used to characterize substrate type, depth and slope along each transect (Grinyó et al., 2016). Seabed substrate types were classified based on an adaptation of the Wentworth scale (Wentworth, 1922) made by Santín et al., (2018): sands, cobbles and pebbles, maërl, and outcropping rock. Seabed slope was classified as horizontal (0–30°), sloping (30–80°) or vertical (80–90°) following the methodology described in Ambroso et al. (2013). Depth was documented as the time reference of any 0.1 m depth variation. Time references were transformed into distances (d) from the beginning of the video transect according to the vehicles speed ($d = t \cdot v$, where t is the time reference expressed in seconds, and v is the velocity expressed in meters per second).

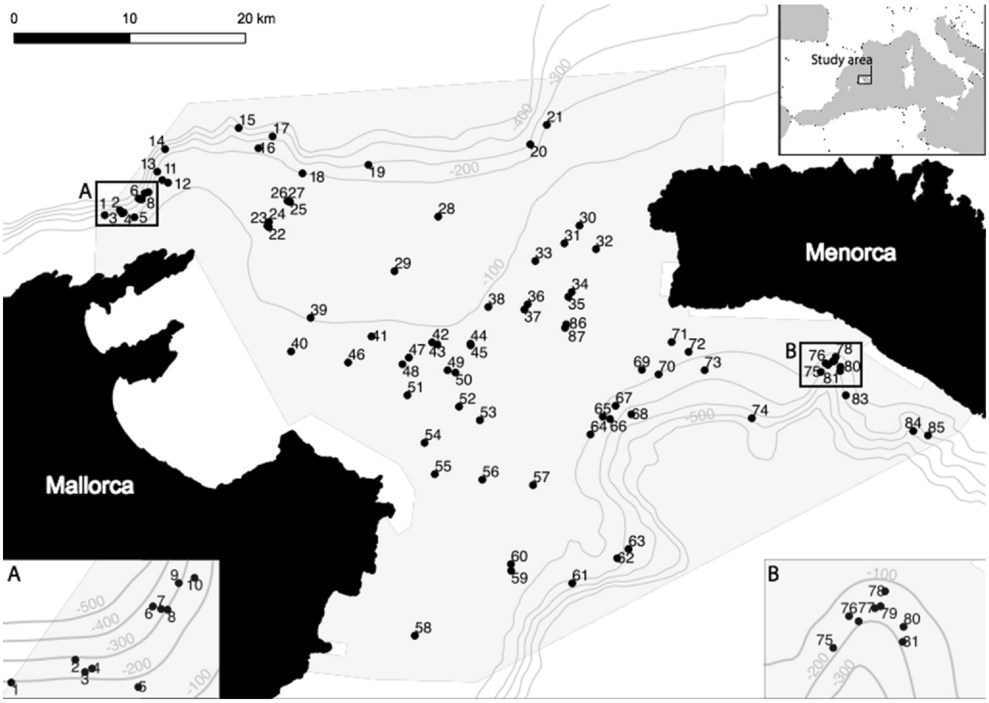

Fig. 1. Location of the video transects in the study area. (A) Enlargement showing video tracks in Cap Formentor; (B) Enlargement showing video tracks in the Menorca Canyon's head. The shaded surface represents the area that covers the Menorca Channel SCI. The location of the survey area in the Mediterranean Sea is shown in the upper right corner.

2.4. Species identification

Identification of soft coral species was based on the existing taxonomic works on Atlanto- Mediterranean soft corals. In order to validate the taxonomic identity voucher colonies of the six soft coral species considered in this study were sampled with the ROVs and manned submersible grab. Sampled colonies were fixed in ethanol 70% or 10% buffered formalin in sea water for morphologic analyses. The encrusting epibiotic species *Alcyonium coralloides* (Pallas, 1766), although present in the study area, was not considered since its occurrence is conditioned by the arborescent anthozoans it colonizes (McFadden, 1999).

2.5. Data treatment

2.5.1. Soft coral occupancy

To quantify soft coral occupancy (frequency of occurrence in the set of sampling units), abundance (number of colonies per sampling unit) and examine species composition of soft coral assemblages, each transect track was divided into equal size fragments, referred to as sampling units of 2 m^2 (0.5 m width and 4 m long) following Gori et al., (2011) methodological approach. This sampling unit dimension was chosen as representative of Mediterranean octocorals on rocky substrate (based on Weinberg, 1978), as well as to allow a comparison with previous studies (e.g. Ambroso et al., 2013; Grinyó et al., 2016). A total of 13,076 sampling units were derived from the division of the 85 video transects. Sampling units were characterized by the number of colonies of each species (density = number of colonies per m^2), as well as by its depth and coverage percentage for each substrate and slope (Grinyó et al., 2018). Following the methodology described in Gori et al. (2011), Ambroso et al., (2013), Grinyó et al. (2016, 2018), Corbera et al. (2019) and Santín et al., (2018, 2019), average densities have been calculated in the subset of occupied sampling units. The reader should be aware that this approach has been selected for the following reason: within a transect, the environmental conditions (e.g., substrate, slope, bathymetric range) can be widely variable. Therefore, if all sampling units within a transect were used to calculate average densities, we would likely be considering sampling units that, due to their environmental conditions, are not suitable for this species occurrence, leading to a density underestimation (e.g. *Alcyonium palmatum* strictly occurs on soft sediments, considering sampling units on hard substrates would underestimate its density). This method guarantees that density is calculated only where species are present and to the authors understanding it provides meaningful ecological information.

2.5.2. Geographical and vertical distribution

The geographical distribution of sampling units holding soft coral colonies, in the study area were registered on a geographically referenced map using GIS (ESRI ArcGIS ArcInfo v10). Vertical distribution of each species was studied grouping sampling units in 20 m depth intervals (based on their depth), and estimating the median (first and third quartile, and the range between minimum and maximum values) of soft coral density in each depth interval.

2.5.3. Assemblage composition and relationships with environmental parameters

Soft coral assemblages were evaluated based on species composition using a non-metric multidimensional scaling ordination (nMDS), soft coral colony abundance data were square root transformed and distances between pairs of samples were calculated using Bray-Curtis dissimilarity index using the *metaMDS* function of the R *vegan* package (Oksanen et al., 2016).

Adonis permutational multivariate analysis of variance were used to test for significance of differences between groups. Adonis was calculated with the *adonis* function of the R vegan packages (Oksanen et al., 2016).

Relationships between soft coral abundances and depth, substrate type and slope were explored by means of canonical correspondence analysis (CCA). This is a constrained multivariate ordination technique for identifying possible relationships between species composition (response variables) and their habitat (explanatory variables) (Greenacre and Primicerio, 2013). Oceanographic variables were not considered as there is no near bottom, long-term, large-scale data set covering the study area. No transformation was applied to either environmental or biological data. The CCA was performed with the function *cca* of the R *vegan* package (Oksanen et al., 2016).

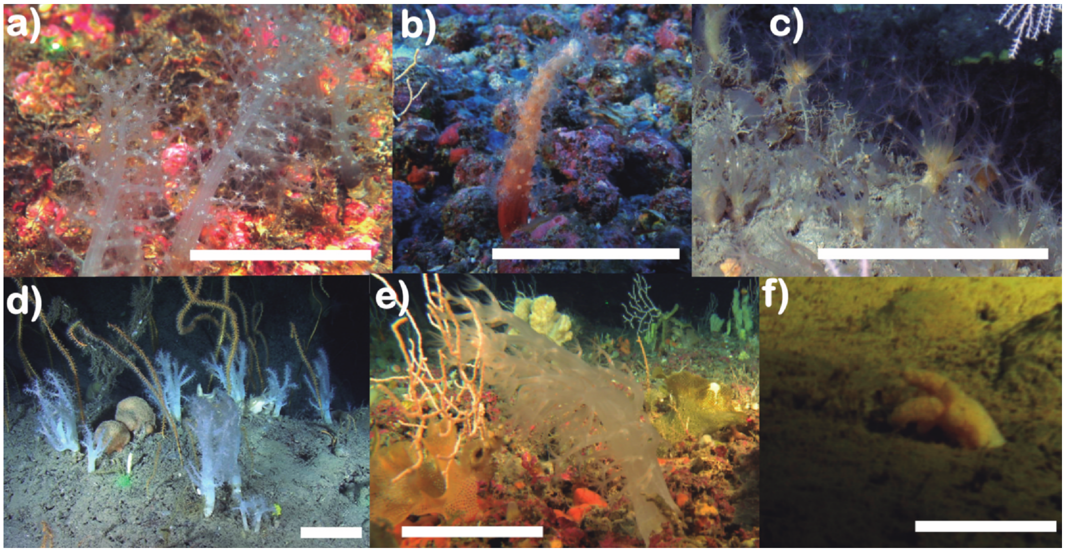

Fig. 2. Studied species images. (a) *Paralcyonium spinulosum*, (b) *Alcyonium* sp., (c) *Nidalia studeri*, (d) *Chironephthya mediterranea*, (e) *Daniela koreni*, (f) *Alcyonium palmatum*. Scale Bar: 10 cm.

3. Results

3.1. Soft corals occupancy and abundance

A total of 9237 colonies of six soft coral species were observed on the study area (Fig. 2 and Table 1), occurring in 9.5% of the 13,076 sampling units. Overall, *Paralcyonium spinulosum* (Delle Chiaje, 1822), *Alcyonium* sp. and *Nidalia studeri* (von Koch, 1891) (Fig. 2a–c) were the most abundant species, respectively representing 55%, 29.4% and 11.5% of all observed colonies. *Chironephthya mediterranea* López-González, Grinyó & Gili, 2014, *Daniela koreni* von Koch, 1891 and *Alcyonium palmatum* Pallas, 1766 (Fig. 2d–f) respectively accounted for 2.1%, 1.8% and 0.2% of observed colonies.

In terms of frequency of occurrence, *Alcyonium* sp., and *P. spinulosum* were the most frequent species occurring on 6.1% and 3% of all sampling units. *C. mediterranea* and *D. koreni* occurred on 0.7% and 0.6% of all sampling units, correspondingly. Finally, *N. studeri* and *A. palmatum* occurred in less than 0.5% of all observed sampling units.

3.2. Geographic and vertical distribution

Four species were observed on continental shelf (40–100 m depth), which were *A. palmatum*, *Alcyonium* sp., *Daniela koreni* and *P. spinulosum*. Here, the two most abundant species were *P. spinulosum* and *Alcyonium* sp., which, respectively represented 67.9% and 32% of the colonies (Table 1). For both species, the highest abundance was observed on the outer continental shelf between 80 and 100 m depth, and shared a similar geographic distribution (Figs. 3 and 4). *Paralcyonium spinulosum* was mainly restricted to the continental shelf at approximately 80 m depth, where it punctually formed highly dense monospecific facies, reaching densities of 60 colonies m^{-2} (Table 1, Figs. 3 and 4, Supplementary material 1). *Alcyonium* sp. was scattered over wide areas of the continental shelf, where it reached its highest densities (18.5 colonies m^{-2}) (Table 1, Figs. 3 and 4).

Daniela koreni occurred throughout the outer continental shelf (80–100 m depth) to the upper continental slope, at the northernmost part of the studied area, near Cap Formentor (Fig. 4). However, most colonies were observed between 96 and 180 m depth, where it reached its highest densities in the shelf edge between 100 and 120 m depth (Fig. 3). *Chironephthya mediterranea* occurred from the shelf edge to the upper continental slope, concentrating in two locations, the Cap Formentor and the Menorca Canyon (Fig. 4). Highest densities were located on shallower environments of the shelf edge, between 100 and 120 m depth, where this species reached densities of 7 colonies m^{-2}

Table 1
Soft coral occupancy and abundance in the study area. Occupancy (frequency of occurrence in the set of sampling units), abundance (number of colonies) and mean and maximum density of each species is given per each bathymetric range. Mean densities have been calculated considering occupied sampling units only.

	Sampling units			Species	Occupancy		Abundance		Mean density ± SD ($col{\cdot}m^{-2}$)	Max density ($col{\cdot}m^{-2}$)
	Num.	With colonies	(%)		Num	(%)	Num	(%)		
Continental shelf (40–100 m)	4362	860	(19.7)	*Paralcyonium spinulosum*	366	(42.6)	5033	(67.9)	6.9 ± 10.5	60
				Alcyonium sp.	624	(72.6)	2367	(32.0)	1.9 ± 2.3	18.5
				Daniela koreni	5	(0.6)	5	(0.1)	0.5 ± 0.0	0.5
				Alcyonium palmatum	3	(0.3)	3	(0.0)	0.5 ± 0.0	0.5
Shelf edge (100 –180 m)	5227	359	(6.87)	*Paralcyonium spinulosum*	22	(6.1)	48	(2.7)	1.1 ± 0.9	3.5
				Alcyonium sp.	174	(48.5)	347	(19.2)	1.0 ± 0.9	5.5
				Nidalia studeri	54	(15.0)	1057	(58.6)	9.8 ± 10	49
				Chironephthya mediterranea	76	(21.2)	179	(9.9)	1.2 ± 1.2	7
				Daniela koreni	71	(19.8)	156	(8.6)	1.1 ± 1.2	7
				Alcyonium palmatum	18	(5.0)	18	(1.0)	0.5 ± 0.0	0.5
Upper slope				*Nidalia studeri*	2	(11.8)	3	(12.5)	0.8 ± 0.4	1
(180–360 m)	3487	17	(0.49)	*Chironephthya mediterranea*	13	(76.5)	18	(75)	0.7 ± 0.3	1
				Daniela koreni	3	(17.6)	3	(12.5)	0.5 ± 0.0	0.5

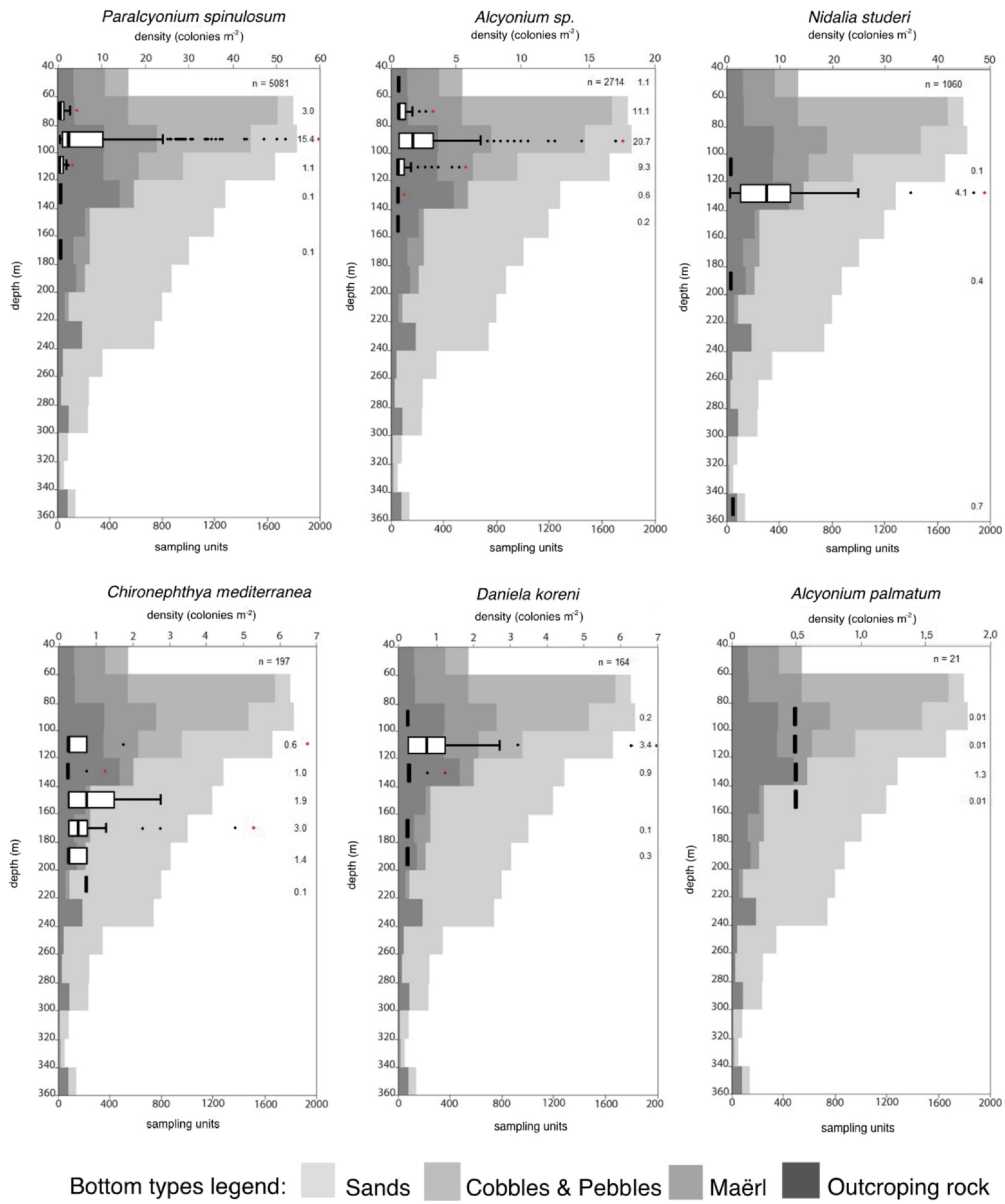

Fig. 3. Vertical distribution. In order of decreasing abundance: *Paralcyonium spinulosum*, *Alcyonium* sp., *Nidalia studeri*, *Chironephthya mediterranea*, *Daniela koreni*, *Alcyonium palmatum* distribution is represented along the studied bathymetric range based on sampling unit density. Black square indicates the median value; the box indicates the first and third quartiles; and the line indicates the range between minimum and maximum values. Gray-scale histograms represent the total number of sampling units for each substrate type (see legend) over the studied bathymetric range. The numbers on the right indicate the percentage of sampling units with species presence (n = number of colonies). Black dots represent lower out layers, red dots represent upper out layers.

(Fig. 3 and Table 1). On the continental slope, *C. mediterranea* was the most frequent and abundant species with few isolated colonies below 210 m depth (Fig. 3). *Alcyonium palmatum* was the species with the narrowest bathymetric distribution occurring at low densities at the northern side of the study area's outer continental shelf (3 colonies at 99 m depth) (Table 1) and shelf edge between 100 and 140 m depth with the highest abundances (Figs. 3, 4 and Table 1).

3.3. Assemblage composition and relationships with environmental parameters

Three soft coral assemblages were differentiated in the nMDS analyses (Fig. 5). Two monospecific assemblages composed by *N. studeri* (Supplementary material 2) and *A. palmatum*; and one multispecific characterized by *P. spinulosum*, *Alcyonium* sp., *C. mediterranea* and *Daniela koreni* (Supplementary material 3), which respectively represented 62.3%, 33.3%, 2.4% and 2% of the colonies in this assemblage (Fig. 5, Supplementary materials 1, 2 and 3). Adonis test revealed that all assemblages were significantly different from one another ($p < 0.001$).

Environmental factors explained 29.2% of the total inertia (explained variation) in the CCA. According to the ANOVA permutation test, the three environmental factors significantly contributed ($p < 0.001$) to the ordination (Fig. 6a). The first two axis of CCA accumulated 25.7% of the species variance and 87.8% of the species-environmental relation variance.

Both monospecific assemblages mostly occurred on shelf edge environments, however while the *N. studeri* assemblage was found on sloping rocky grounds, the *A. palmatum* assemblage occurred on

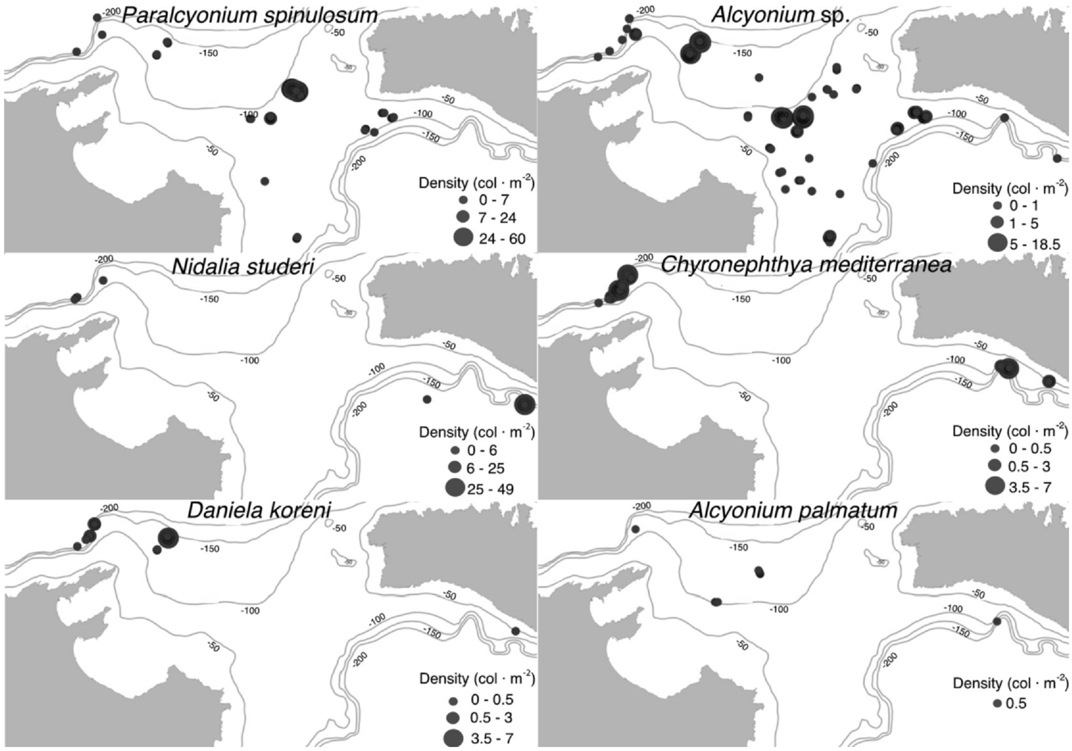

Fig. 4. Geographical distribution of soft coral species, represented in order of decreasing abundance. Distribution is represented on the study area based on sampling unit density.

horizontal sandy bottoms (Figs. 5 and 6). The multispecific assemblages were found on horizontal maërl beds and rocky outcrops along the continental shelf and shelf edge (Figs. 5 and 6).

4. Discussion

4.1. Soft coral diversity and abundance:

Soft coral diversity values are higher than those reported in shallow and other mesophotic and deep Mediterranean environments where less than three species are generally present (Ambroso et al., 2013; Topçu and Öztürk, 2015; Casas-Güell, 2016; Bo et al., 2011; Pierdomenico et al., 2016, Cau et al., 2017a, Corbera et al., 2019; Enrichetti et al., 2019b). In this sense, the Menorca Channel is one of the richest areas in terms of soft coral diversity, known so far, in the Mediterranean Sea. Along the explored bathymetric range highest soft coral diversity was found on the shelf edge, where all species were present (Figs. 3–5). These high diversity values in shelf-edge environments could derive from the merging of species with shallow and deep distributions, resulting in a mid-domain effect (Colwell and Lees, 2000), resembling diversity trends observed on octocoral assemblages on other areas of the world (Matsumoto et al., 2007). In this regard, gorgonian diversity in the study area also presented its highest diversity values on the shelf edge (Grinyó et al., 2016). Conversely, highest sponge diversity was found on the outer continental shelf (Santín et al., 2018, 2019). The fact that anthozoan and porifera diversity patterns differ from one another could indicate that different environmental factors drive passive and active suspension feeder distribution in the Channel.

Total abundances in the study area were remarkable; a total of 9360 colonies were recorded over 72 km clearly exceeding total abundances in more extensively explored environments such as Newfoundland canyons where 8757 soft coral colonies were recorded over 105.3 km

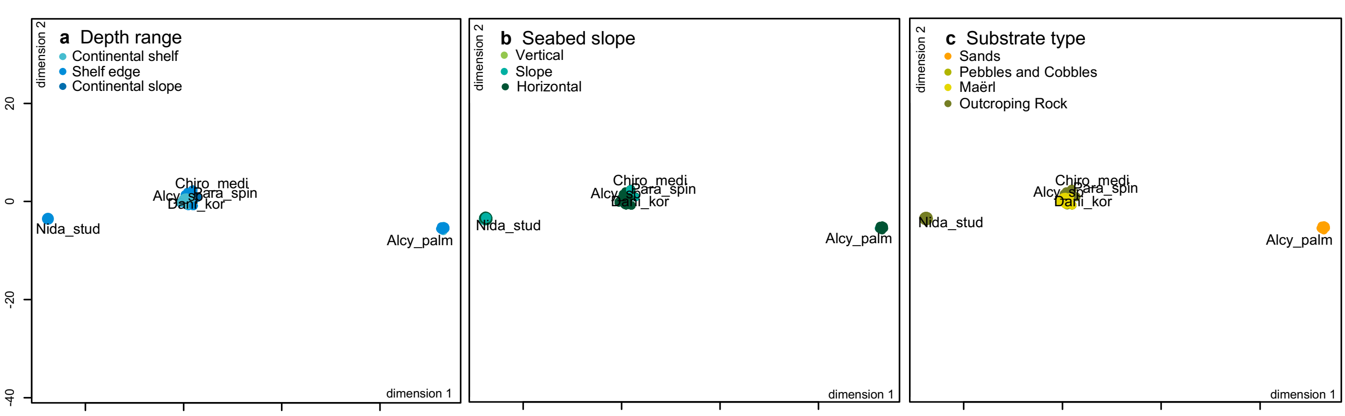

Fig. 5. Non-metric multidimensional scaling (nMDS) ordination plot. Sampling units (n = 1236) containing soft corals are represented considering a) depth, b) slope and c) substrate types. A stress estimate of 0.0024 was obtained. Alcy_sp = *Alcyonium* sp., Alcy_palm = *Alcyonium palmatum*, Chiro_medi = *Chironephthya mediterranea*, Dani_kor = *Daniela koreni*, Nida_stud = *Nidalia studeri*, Para_spin = *Paralcyonium spinulosum*.

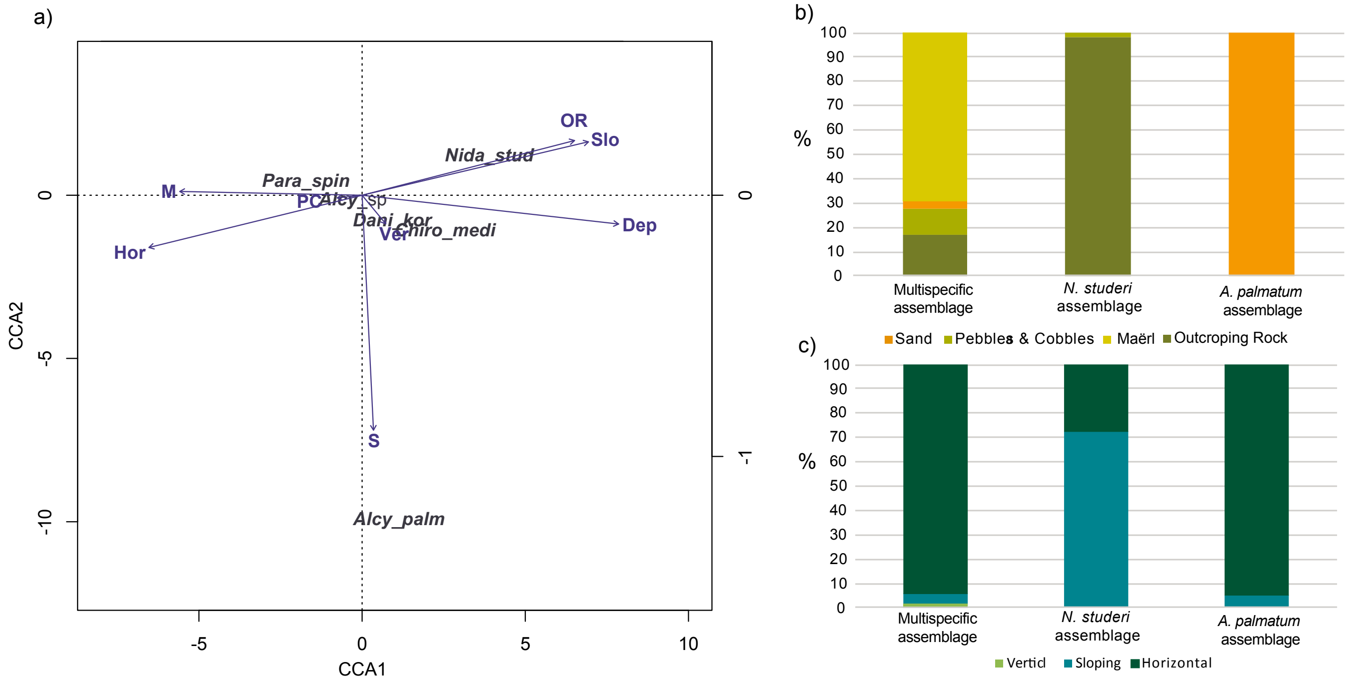

Fig. 6. Soft coral assemblage relationship with environmental factors. a) Canonical correspondence analysis (CCA): biplot showing the ordination of soft coral species and the roles of the significant environmental variables. M: Maërl, S: Sand, CSP: cobbles and pebbles, OR: Outcropping rock, Slo: Sloping, Hor: Horizontal, Ver: Vertical, Dep: Depth. Alcy_sp = *Alcyonium* sp., Alcy_palm = *Alcyonium palmatum*, Chiro_medi = *Chironephthya mediterranea*, Dani_kor = *Daniela koreni*, Nida_stud = *Nidalia studeri*, Para_spin = *Paralcyonium spinulosum.* Column charts representing each assemblage sampling unit percentage occupied by a certain b) substrate or c) slope.

(Baker et al. 2012). Compared to other Mediterranean anthozoans average soft corals densities were within the same range as several gorgonians found in the Mediterranean continental shelf and slope (Grinyó et al., 2016), but exceeded those reported for other deep Mediterranean anthozoans such as the bamboo coral *Isidella elongata* (Esper, 1788) (Bo et al., 2015; Pierdomenico et al., 2018; Ingrassia et al., 2019), pennatulaceans (Grinyó et al., 2018; Chimienti et al., 2018b; Pierdomenico et al., 2018), antipatharians (Bo et al., 2009, 2014, 2015; Cau et al., 2015; Corbera et al., 2019), and solitary and framework-building scleractinians (Orejas et al., 2009; Corbera et al., 2019). Soft corals tent to present smaller colony dimensions, than the previously mentioned CWCs, which could allow them to form more densely packed aggregations (McFadden, 1986). This would agree with the fact that highest Mediterranean CWC densities have been reported among small sized species (< 20 cm) that form dense monospecific aggregations, such as the hydrocoral *Errina aspera* (Linnaeus, 1767), that can reach densities of 445 col·m^{-2} (Salvati et al., 2010). In this regard, in the study area *N. studeri* and *P. spinulosum* punctually formed dense monospecific aggregations reaching densities of 49 and 60 col·m^{-2}, respectively (Table 1; Supplementary material 1 and 2). These monospecific aggregations extended over several hundreds of meters where both species monopolized substrate representing > 90% of all observed sessile megabenthic species. In this sense, Enrichetti et al., (2019b) have recently described *P. spinulosum* fields in the Ligurian Sea where this species reached densities of 76.6 col.·m^{-2}. Similarly, on the North Atlantic and North Pacific, soft corals have also been reported to form dense beds monopolizing space (Bulh-Mortensen et al., 2015; Yoklavich et al., 2018). These densely packed monospecific aggregations have been suggested to derive from both vegetative mechanisms, such as fission and migration (Benayahu and Loya, 1986; McFadden, 1986), and certain reproductive strategies, such high fertility rates and large lecithotrophic larvae (Yoklavich et al., 2018), which may increase colonization success. However, this topic requires further investigation as most biological aspects of the species evaluated in this study remain unknown.

4.2. *Soft coral assemblages:*

Assemblage composition analysis revealed three soft coral assemblages, which were mostly segregated by depth and substrate and to a lesser extent slope (Figs. 5 and 6). The multispecific soft coral assemblage occurred along the continental shelf and shelf edge (Figs. 3–5) on rocky outcrops (17% of occupied sampling units), but mostly on maërl beds (70% of occupied sampling units) (Fig. 6). Overall soft coral density was significantly higher (Adonis, $p < 0.001$, Pseudo-F = 16.22) on maërl beds (11.2 ± 15.2 col.·m^{-2} (mean ± SD)) than on rocky substrates (5.2 ± 5.4 col.·m^{-2} (mean ± SD)). This would indicate that deep maërl beds are a particularly suitable habitat for deep Mediterranean soft corals species, resembling multispecific soft coral assemblages on mesophotic rhodolite beds in subtropical and tropical environments (Richards et al., 2013; Linklater et al., 2019). Contrastingly, previous studies have suggested that the presence of arborescent anthozoans, on maërl beds may be limited by substrate instability, which under intense currents may derive in colony toppling (Kahng et al. 2010). However, unlike most arborescent anthozoans, soft-corals have the capacity to contract their colonies. In this sense, it has been observed that under strong water flows soft corals tend to contract their colonies, substantially reducing their dimensions and resistance to water flow (Fabricius et al., 1995), which may allow them to thrive in this unstable substrate.

The densely packed *N. studeri* assemblage was also found on hard substrates of the shelf edge. Unlike the multispecific assemblage that was restricted to horizontal grounds, the *N. studeri* assemblage was generally restricted to sloping grounds (72% of occupied sampling units) (Figs. 5 and 6). Ecological information about this species is quite scarce, however in recent years sightings of this rediscovered species have increased all over the western Mediterranean expanding their geographic extent and bathymetric distribution, which has now been extended to 600 m depth (Oliveri et al., 2016; Aguilar et al., 2017; Álvarez et al., 2019). In most cases, *N. studeri* has been observed to occur on hard substrates as isolated colonies or forming small aggregations over a wide bathymetric range (Álvarez et al., 2019). However, on the Gulf of Naples this species was described to dominate certain areas of the continental slope below 300 m depth (Oliveri et al., 2016) resembling *N. studeri* aggregations in the study area.

The *A. palmatum* assemblage was restricted to soft sediment grounds on the outer continental shelf and the shelf edge where this species sparsely occurred (Figs. 4–6). In the study area, *A. palmatum* presented similar density values as in areas of the inner continental shelf of the North Western Mediterranean (Ambroso et al., 2013), however its distribution was narrower than in other areas of the northwestern Mediterranean where this species has been reported between 40 and 120 m depth (Gili et al., 2011). In the study area fine soft sediments were mainly found between 100 and 140 m depth on the northern site of the Channel. In other areas of the Mediterranean, *A. palmatum*'s occurrence has been associated to fine sediments (Galil and Lewinsohn, 1981; Sardá et al., 2012; Ambroso et al., 2013). Currently, very few studies have considered granulometry among the environmental factors that might explain anthozoan distribution in soft sediment environments (Orejas et al., 2019). Future studies should address if *A. palmatum*'s distribution is related to a certain grain size.

4.3. Conservation remarks

Due to their three-dimensional, branched morphology and soft colonial consistence, soft corals are particularly vulnerable to fishing activities (Mytilineou et al., 2014; Bo et al., 2015). In several areas of the Mediterranean various soft corals (genus *Alcyonium* sp., especially *Alcyonium palmatum*) have been commonly observed associated to lost fishing gears on Mediterranean continental shelf (Voultsiadou et al., 2011; Angiolillo et al., 2015) or as main components of fishing bycatch (Dimitriadis et al., 2016). Among the different fishing practices bottom trawling is the most harmful for anthozoan assemblages (Althaus et al., 2009). In the Menorca Channel, trawling has mostly been restricted to areas above 75 m and below 500 m depth (Grinyó et al., 2018). It is likely that the high soft coral diversity observed in the study area and the massive aggregations of *P. spinulosum* and *N. studeri*, may respond to low trawling pressure within the explored depth range. Derelict longlines, trammel and gill nets have also been reported to cause impacts on anthozoan assemblage (Cau et al., 2017b; Calgani et al., 2018; Enrichetti et al., 2019a). Although, no soft coral colony was observed to be damaged by derelict fishing gears, future studies should address the potential negative effects that fishing practices may cause in the studied soft coral assemblages in order to develop and implement management plans that ensure their preservation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2020.102435.

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