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Facies created by the yellow coral *Dendrophyllia cornigera* (Lamarck, 1816): origin, substrate preferences and habitat complexity

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Abstract

The yellow coral *Dendrophyllia cornigera* (Lamarck, 1816) is a NE Atlantic-Mediterranean scleractinian and it is considered a typical hard bottom species, generally reported on outcropping rocks from mesophotic to upper bathyal depths. Several evidences suggest that this species is able to tolerate a broad range of temperatures, which allows it to colonize numerous environments in a wide depth range.

In the present study, we first provide a detailed ecological characterization of the *D. cornigera* dense aggregations thriving on the Mantice Shoal (NW Ligurian Sea, Mediterranean Sea). Information on substrate type and inclination, average extension and density, colonies size-class frequency distribution and associated fauna are reported. Then, we present an extensive review of the available information on the ecology of this species, including 142 new ROV records from the Italian coast (40-1820 m). Results indicate that *D. cornigera* occurs on a wide range of substrates, including soft bottoms and hardgrounds (outcropping rocks, coralligenous rock and dead cold-water coral frameworks), with significant differences in colony density and size among different substrates.

Dendrophyllia cornigera creates three main facies, each characterized by a specific combination of substrate, inclination, depth, and associated fauna. Scattered living colonies as well as large thanatocoenoses display a wide geographical and bathymetric distribution. Differently, the facies represented by dense meadows on horizontal soft-bottoms results rare, being reported only from the Mantice Shoal and the Amendolara Bank (Ionian Sea). Radiocarbon age of the thanatocoenoses varies between 400 (Corsica Channel) and 13000 (Vercelli Seamount) years before present.

This study highlights the wide adaptability of *D. cornigera* in terms of environmental settings, changing the current view on the ecology of this species, and providing essential insights for the implementation of international deep-sea habitat classification schemes and conservation measures.

Keywords

Dendrophylliidae, Cold-Water Corals, thanatocoenoses, mesophotic, upper bathyal, Ligurian Sea, Mediterranean Sea.

1. Introduction

The yellow coral *Dendrophyllia cornigera* (Lamarck, 1816) is a colonial scleractinian characterized by a sparse irregular branching, a bright color of the coenenchyma and size up to 40 cm (Zibrowius, 1980; Fourt et al., 2017). Like all the other members of the family Dendrophylliidae, whose monophyly has been confirmed by Arrigoni et al. (2014), this species is characterized by porous walls and a peculiar arrangement of septa in triangles (the so-called Pourtalès plan) (Cairns, 2001). In the Mediterranean Sea, this family accounts for eight species, four of which inhabit deeper waters, namely *Balanophyllia cellulosa* Duncan, 1873, *D. cornigera*, *Dendrophyllia ramea* (Linnaeus, 1758) and *Leptopsammia pruvoti* Lacaze-Duthiers, 1897. Both *B. cellulosa* and *L. pruvoti* present a solitary corallum and differ from each other in their septa arrangements and ecological preferences (Altuna and Poliseno, 2019). In contrast, *Dendrophyllia* species are colonial and form three-dimensional structures growing by extra-tentacular budding. *Dendrophyllia ramea* is commonly known as pink coral and forms arborescent colonies up to 1 m in height with more regular branching with respect to *D. cornigera* (Zibrowius, 1980).

Both *D. cornigera* and *D. ramea* result widely distributed in the NE Atlantic and Mediterranean Sea. *D. ramea* has been reported in the Atlantic Ocean from the Gulf of Cadiz, Azores and Canary Islands, whereas in the Mediterranean Sea it is mainly recorded in the southern area of the western basin (Salvati et al., 2021). It ranges from shallow waters (Salvati et al., 2004; Cinar et al., 2014) to 170 m depth (off Cyprus and off East Sardinia) (Bonfitto et al., 1994; Orejas et al., 2017), with only one deeper population (240 m) known from the Menorca Channel (Jiménez et al., 2016); generally, however, it is reported shallower than 100 m depth, in the circalittoral realm (Orejas et al., 2019a). *D. cornigera* distribution is wider, spanning in the Atlantic Ocean from the Celtic Sea to the Azores Islands and Cape Verde Islands, and resulting common in the whole western Mediterranean basin, as well as along the Sicily Channel, Ionian Sea, South Adriatic and Aegean seas (Freiwald et al., 2009; Orejas et al., 2009; Salomidi et al., 2010; Bo et al., 2011, 2014a; Gori et al., 2013, 2014; Castellan et al., 2019; Chimienti et al., 2019). *D. cornigera* bathymetric range extends from 70 to 733 m in the Mediterranean Sea and from 30 to 1200 m in the Atlantic Ocean, representing a considerable component of both mesophotic and deep coral ecosystems (Castellan et al., 2019). The wide spectrum of environments populated by *D. cornigera* has been related to the capacity to maintain its physiological functions in a broad range of temperatures (from 7°C to 17 °C), indicating less restrictive environmental needs if compared to other cold-water coral species (Roberts et al., 2006; Gori et al., 2014; Castellan et al., 2019; Reynaud and Ferrier-Pagès, 2019).

Le Danois (1948), based on the still scarce information available for the eastern Atlantic Ocean, reported that *D. cornigera* only settles on rock and it avoids muddy bottoms. In the Mediterranean

Sea, Pérès and Picard (1964) considered *D. cornigera* and *D. ramea* typical hard-bottom species, characteristic of the circalittoral "offshore deep rock community". At present, the two species are still largely considered typical of hard bottoms. More specifically, *D. cornigera* is commonly reported with scattered colonies on flat to gently sloping outcropping rocks, boulders, or biogenic frameworks (Hebbeln et al., 2009; Orejas, 2009; Bo et al., 2012; Fabri et al., 2014; Altuna and Poliseno, 2019; Chimienti et al., 2019). Curiously, *D. cornigera* has been seldom reported on soft bottoms, mainly at mesophotic depths, indicating that the broad adaptability of this species can be also extended to its substrate preferences (Michez et al., 2014). Particularly interesting is the population of the Maledetti Shoal (Ligurian Sea, NW Mediterranean Sea), where it is reported to form an extended and dense meadow on silted detritic bottoms (up to 15 col m^{-2}) (Bo et al., 2014a; Enrichetti et al., 2019). Furthermore, large beds of dead *D. cornigera* have also been reported forming extended thanatocoenoses, generally at bathyal depth (Zibrowius, 1980; Taviani et al., 2005; Hebbeln, 2009; Bo et al., 2011, 2014b; Pardo et al., 2011; Vertino et al., 2014). Age information on these thanatocoenoses is scarce, but when available, it generally dates back to the Pleistocene, when the diversity and abundance of Mediterranean dendrophylliids were much higher (Vertino et al., 2014, 2019; Corbera et al., 2021). Such information suggests that the original view of *D. cornigera* as a typical hard-bottom species is simplistic and that this species can create a variety of facies associated with different habitats and substrates at mesophotic and bathyal depth, supporting more comprehensive conservation issues.

The aim of the present study is to investigate the different facies created by *D. cornigera*, with specific reference to the substrate type on which they develop. To fill this gap, we first provide a detailed characterization of the peculiar *D. cornigera* population of the Mantice Shoal, with information on spatial and bathymetrical extension, substrate type, inclination, density and size-class frequency distribution. Then, aiming to characterize the overall distribution and the ecological characteristics of the different facies created by this species, a comprehensive analysis of the available information on *D. cornigera* records throughout its geographical range is provided, including literature data and new unpublished records. Finally, to better understand the origin of the extended *D. cornigera* thanatocoenoses, coral rubble samples have been collected from different Mediterranean bathyal areas and dated through radiocarbon isotopes.

2. Materials and methods

2.1 The Mantice Shoal

The Mantice Shoal is located in the Ligurian Sea (NW Mediterranean Sea), about 3 nautical miles SE off the large harbor of Savona (Fig. 1a). The shoal is approximately 600 m long and 100 m wide and it is composed of a series of NE/SW orientated, highly silted, sub-outcropping and outcropping rocks. The shoal develops on a sloping soft bottom ranging from 80 to over 150 m depth, with the shoal summit reaching -78 m in its shallowest parts (Fig. 1b). A 300 m wide channel separates the shoal from the continental break, here located at about 70 m depth (Wurtz et al., 2012).

The main circulation in the Ligurian Sea flows westward (Millot, 1999; Cattaneo-Vietti et al., 2010). Casella et al. (2011) demonstrated that anti-cyclonic mesoscale and sub-mesoscale eddies remain trapped between the main current and the coastline, causing strong upwelling events that support an elevated spring primary production. Furthermore, the presence of the Vado Canyon in the area of the Mantice Shoal causes the upwelling of deep water, providing additional amount of nutrients. As a result, the megabenthic communities of this area result rich and dominated by suspension feeders, especially anthozoans (Bo et al., 2014a; Enrichetti et al., 2019). The outcropping rocks of the shoal are dominated by dense forests of the gorgonian *Eunicella cavolini* (Koch, 1887) reaching densities of up to 22.4 colonies m^{-2}. Associated structuring species include other gorgonians, such as *Paramuricea clavata* (Risso, 1826) and *Eunicella verrucosa* (Pallas, 1766), the black coral *Antipathella subpinnata* (Ellis Solander, 1786) and scattered colonies of the yellow coral *D. cornigera*. The soft bottoms surrounding the Mantice Shoal host aggregations of the large hydrozoan *Lytocarpia myriophyllum* (Linnaeus, 1758), fields of the soft coral *Paralcyonium spinulosum* (Delle Chiaje, 1822) and dense meadow of *D. cornigera*, with density of up to 15 colonies m^{-2} (Fig. 1c). This population of *D. cornigera* has been reported as the largest and northernmost in the whole Mediterranean basin (Enrichetti et al., 2019), although no detailed characterization has been carried out so far.

2.2 Characterization of the **D. cornigera** *population of the Mantice Shoal*

The *D. cornigera* meadow of the Mantice Shoal has been investigated by means of multibeam echosounder (MBES) and remotely operated vehicle (ROV). High resolution (1 m) bathymetric data were collected in 2015 from the *R/V Astrea* (ISPRA) using a hull-mounted Kongsberg EM 2040 MBES, operating at a frequency of 300 kHz. In addition, four ROV dives (E07, E08, E09, E10) were carried out between 2012 and 2015 (Tab. 1; Fig. 1b): technical specifics of ROV, tracks and video analysis can be found in Enrichetti et al. (2019). The video time code associated with the beginning and the end of each coral patch allowed to map their occurrence through QGIS software (version 3.22). The length of each patch was measured, and the analyzed surface was calculated by multiplying the length and the width of the video transect (0.5 m), allowing to determine mean (±SE) and maximum abundance (as no. of colonies m^{-2}).

In addition, information on bathymetric range, seabed inclination, substrate type and associated megabenthic species were annotated. To provide a better characterization of the megabenthic communities inhabiting the soft bottoms of the shoal, the aggregations of *L. myriophyllum* and *P. spinulosum* were also mapped. To better figure the topography of the Mantice Shoal and the distribution and putative extension of the *Dendrophyllia* patches, terrain profiles were plotted using the profile tool plugin available on QGIS software (version 3.22).

D. cornigera maximum and mean (±SE) sizes were investigated measuring 300 specimens randomly selected from the ROV photo footage. Parallel laser beams mounted on the ROV provided a scale for dimensional reference. In addition, the size-class frequency distribution of the whole population was calculated. Finally, overturned colonies, broken branches and changes in polyp's orientation were annotated to evaluate the anthropic impact.

2.3 Large-scale characterization of **D. cornigera**

To provide a comprehensive characterization of the ecology of *D. cornigera* throughout its whole distribution range, a large dataset was created including information from two separate sources. First, an extended bibliographic research was carried out on the on-line platforms Scopus and Google Scholar. The reference lists included in the downloaded papers were also checked and, when relevant, included in the dataset. Additionally, new information on *D. cornigera* distribution and ecology was gained analyzing video and still-images collected during 645 ROV dives carried along the Italian coast from 2006 to 2021. This archive covers a broad bathymetrical and geographical range, spanning from 40 to 1820 m, and includes continental and offshore locations in the Ligurian Sea, the Tyrrhenian Sea, the southern and eastern coast of Sardinia, the Sicily Channel, the Ionian Sea and the South Adriatic Sea.

Bibliographic and ROV materials were analyzed searching for information regarding *D. cornigera* spatial and bathymetrical distribution, type of substrate, inclination, and type of aggregation created. Substrate type was defined according to the following categories: i) outcropping and sub-outcropping rocks, ii) coralligenous rocks (mainly referring here to deep rocks covered in crustose coralline algae, CCA) and maërl iii) dead cold-water corals, and iv) sandy or muddy soft bottoms. The substrate inclination was also determined using three categories: horizontal (< 20°), sloping (20°-70°) and (sub)vertical (> 70°). In addition, the type of aggregation created by *D. cornigera* have been categorized as: i) scattered living colonies, ii) dense meadow of living colonies, iii) thanatocoenosis without living colonies, iv) thanatocoenosis with some scattered living colonies, and v) thanatocoenosis and dense meadow of *D. cornigera*. To provide an overview of the geographical distribution of the different facies created by *D. cornigera* and its occurrence on different substrates, results were mapped on a QGIS project (version 3.22).

The large ROV archive of the Italian coast was analyzed to detect variation in *D. cornigera* density and size. Ten pictures targeting high-density patches of *D. cornigera* were selected for each site where living colonies were observed. Density estimations (no. of colonies m^{-2}) were provided by dividing the number of colonies for the picture area. Mean (± SE) values were calculated for each site and for each substrate category. In addition, all the *D. cornigera* colonies observed within each picture were measured using Image J software (version 1.53o – 11th January 2022). ROV lasers provided scale references for picture areas and colonies height estimations. Maximum and mean (±SE) sizes, as well as size-frequency distributions, were calculated for each substrate type. A Kruskal-Wallis test was performed to identify significant differences in *D. cornigera* density and size among substrate types (SB, soft bottom; OR, outcropping rock; CR, coralligenous rock; dCWC, dead *Lophelia/Madrepora* corals), with n = 60 – 855 for the density dataset, and n = 23 – 791 for the size dataset (data not normally distributed, not transformed, with p = probability, H = Kruskal-Wallis statistic). Then, to identify which groups were significantly different from each other, a Dunn's *post-hoc* test was carried out using raw p values and sequential Bonferroni significance. Statistical analyses were performed using PAST for Mac (version 3.20) (Hammer et al., 2001).

Finally, all the megabenthic species observed in the analyzed pictures were annotated, aiming to characterize the fauna associated with each *Dendrophyllia* facies.

2.4. Radiocarbon dating

Five dead coral branches of *Dendrophyllia cornigera* were used for radiocarbon dating (Hajdas et al., 2021). Coral branches were collected by ROV or as a fishing bycatch from deep-sea thanatocoenoses along a wide latitudinal range (Ligurian Sea, Tyrrhenian Sea and Sicily Channel) (Tab. 2). Analyses were carried out by AMS (Accelerator Mass Spectrometry) at CEDAD (Centre of Applied Physics, Dating and Diagnostics), University of Salento, Italy (Calcagnile et al., 2019). Samples were submitted to standard processing procedures (Calcagnile et al., 2004). The measurement of $^{14}C/^{12}C$ and $^{13}C/^{12}C$ isotopic ratios were used to calculate conventional radiocarbon ages according to Stuiver and Polach (1977). Conventional radiocarbon ages were then calibrated to calendar years by using the Marine20 calibration curve valid for marine data (Heaton et al., 2020) and the OxCal Vers. 4.3 Software (Ramsey, 2001). A local reservoir correction $\Delta R = -158 \pm 23$ years was used obtained for the Northern Tyrrhenian sea (Faivre et al., 2019; Quarta et al., 2021).

3. Results

3.1. The **Dendrophyllia cornigera** *population of the Mantice Shoal*

Dendrophyllia cornigera is widespread on the Mantice Shoal, on both hard and soft bottoms. On the rocky outcrops, it is observed between 80 and 160 m depth on flat, sloping and almost vertical substrates generally associated with *Eunicella cavolini* forests (Fig. 2a). In addition, *D. cornigera* patches are occasionally observed on bare rocks with encrusting sponges, solitary scleractinians, serpulids and echinoderms (Fig. 2b). The maximum density calculated on hard bottoms accounts for 2.14 colonies m^{-2}.

A total of eight *Dendrophyllia cornigera* patches were observed on the soft bottoms of the Mantice Shoal (Table 1, Fig. 1c, 2c-l; Supplementary Material 1). Their average linear extension, calculated following the ROV path, accounts for 56.1 m ± 28.3 m. Five patches, including the largest ones (132 and 225 m long), occur in the North-eastern part of the shoal, on a sloping terrigenous muddy bottom (about 30°) located between 83 and 118 m depth (Fig. 1c, 3a; Supplementary Material 1). The smallest patches, 1.7 and 3.8 m long, respectively, occur in the South-western portion of the shoal: they lie between 83 and 96 m depth, on muddy bottoms among sub outcropping rocks rich in biogenic detritus and characterized by moderate inclination (20°-45°) (Fig. 3a). One additional patch occurs on the norther side, in the channel separating the shoal from the continental break. It is about 20 m long and is located at 100-102 m depth on a sub-horizontal muddy bottom near sub-outcropping rocks.

Overall, all the *Dendrophyllia* patches develop on soft bottoms with inclination ranging between 5° and 45°. The soft bottom results composed by terrigenous mud and variable amount of biogenic detritus (Fig. 2c-l). The aggregations located among the outcropping rocks of the Mantice Shoal present a larger amount of biogenic detritus, mainly represented by calcareous bryozoans remains. On the contrary, the large meadow located on the northeastern slope are mainly characterized by sparse *Dendrophyllia* rubble and bivalve shells.

Within the patches, *Dendrophyllia* colonies are generally up-right orientated, with the basal part buried in the sediment and the bright-yellow living polyps exposed at the top of the branches (Fig. 2c-d), but overturned or broken colonies result common. In the 9% of the analyzed colonies (n = 300), in fact, living polyps are observed reorganizing their orientation to avoid silt clogging (Fig. 2e-i). The fact that colonies are not anchored beneath the sand, if not to very small cobbles or biogenic detritus, was confirmed also through sample collection. *D. cornigera* density, calculated from the ROV paths, can vary among and within the patches, ranging between 0.4 and 11.6 colonies m^{-2}. The highest density values are encountered within the large meadows of the northeastern slope, where high-density and low-density patches alternate (Tab. 1). The analysis of 300 colonies indicates that the average height accounts for 7.1 ± 0.3 cm, with minimum and maximum values being 0.7 and 27.4

cm. The size-class frequency distribution reveals a unimodal distribution, with the second size class (5-10 cm) being the best represented (47%), followed by the smallest one (0-5 cm; 34%) (Fig. 3b). Up to 24 megabenthic species have been recorded within the *Dendrophyllia* patches (Fig. 2d, e, g, j-l), mainly belonging to cnidarians (six species), poriferans (five species), echinoderms and fishes (four species), and annelids (two species). Mollusks and arthropods account for two and one species, respectively. Cidarid sea urchins represent the most common (occurring in 63% of the patches) and abundant (74 individuals) associated species. Tube-anemones, the sabellid polychaete *Myxicola* sp. and the serpent eel *Ophisurus serpens* (Linnaeus, 1758) are also reported. The dead portions of *Dendrophyllia* colonies are often covered by encrusting sponges, solitary scleractinians, newly-settled colonies of the gorgonian *Eunicella cavolini*, and serpulid tubes (Fig. 2e, g, l).

3.2. **Dendrophyllia cornigera** ***global distribution, substrate preferences and facies***

The bibliographic research produced a total of 241 *D. cornigera* records from the NE Atlantic and the Mediterranean Sea, obtained from 43 publications spanning from 1873 to present (Fig. 4; Supplementary Material 2). Four additional publications, containing 26 records from South Africa and the Indian Ocean (Fig. 4 inset) were not considered here. Overall, 98% of the records included depth information, whereas substrate type and inclination were reported only in 43% and 31%, respectively. General indication on type of aggregation was specified in 51% of the records. The analysis of the ROV archive produced 142 additional records of *D. cornigera* along the Italian coasts, for a total of 383 records distributed from the Celtic Sea to Senegal and from the Azores Islands to the Aegean Sea (Fig. 4).

Figure 5a shows the NE Atlantic-Mediterranean distribution of *D. cornigera* according to substrate type. The majority of the records (83%) indicates that this species commonly settles on hard substrates, being generally represented by outcropping rocks (63%) (Fig. 5b). In the Mediterranean Sea, *D. cornigera* is often reported on coralligenous rocks, with only one record occurring from the E Atlantic (off St. Jago Island, Cabo Verde) (Moseley, 1881). *D. cornigera* on rocks covered by CCA (12%) results particularly common in the Tyrrhenian Sea, especially on the summit of euphotic seamounts (e.g., Vercelli, Palinuro), offshore islands (e.g., Pontine and Aeolian archipelagos), and along the coast of southern Sardinia and Calabria (Fig. 5c). The only record of *D. cornigera* associated with maërl beds comes from the Aegean Sea (Vafidis et al., 1997). *D. cornigera* has also been observed growing on dead *Madrepora*/*Lophelia* colonies (8%) (Fig. 5d) in the Bari Canyon, Santa Maria di Leuca, Corsica Channel, Sardinia, Alboran Sea, Grande Vasièr Bank and off Morocco. Records on soft bottoms are common (17%) (Fig. 5e), occurring from both the Mediterranean Sea (Gulf of Lions, Ligurian Sea, Tyrrhenian Sea, Sicily Channel, Ionian Sea, and Aegean Sea) and NE

Atlantic (Bay of Biscay, Cantabrian Sea, and off Morocco). The majority of *D. cornigera* records (55%) occurs on sloping bottoms, ranging between 20° and 70°, followed by horizontal bottoms (37%). Records on vertical substrates account for 8%. In addition, regarding associated fauna, encrusting sponges, hydrozoans, solitary scleractinians (e. g. *Caryophyllia* spp.), serpulids tubes, and cidarids sea urchins resulted the most common taxa found with *D. cornigera*. These species settle on hard substrates among the colonies or colonize the dead portions of the coral branches. Beside these common species, other species have been reported as typical from each *Dendrophyllia* facies.

D. cornigera aggregations can be classified into two major groups, one dominated by living colonies and the other dominated by dead remains. Living aggregations are represented by i) sparse living colonies and ii) dense meadows (Fig. 6), while dead aggregations are represented by different types of thanatocoenoses (iii, iv, and v).

Sparse living colonies (i) represent the most frequent category (71% of the whole dataset), generally being reported from deep shelf banks and canyon rocky terraces in all the investigated sub-basins (Fig. 6a, b; Fig. 2a, b). Colonies generally develop on outcropping rocks, but also on CCA-covered rocks and cold-water coral frameworks with sloping or sub-horizontal inclinations (Fig. 7a, b). More rarely, they have been reported on soft bottoms or on vertical hard bottoms. In this case, *D. cornigera* is not the dominant species, but it often participates to other biocoenoses, for example those characterized by sponges (e.g. *Axinella* spp., *Pachastrella monilifera* Schmidt, 1868, *Rhabderemia* sp.), gorgonians [e.g., *Callogorgia verticillata* (Pallas, 1766), *Corallium rubrum* (Linnaeus, 1758), *Eunicella cavolini* (Koch, 1887)], black corals [e.g., *Antipathes dichotoma* Pallas, 1766, *Antipathella subpinnata* (Ellis Solander, 1786)], and brachiopods [e.g., *Megerlia truncata* (Linnaeus, 1767)].

Dense meadows of living *D. cornigera* (ii) have been reported only from two sites (1% of the records): the horizontal soft bottoms surrounding the Mantice Shoal (Ligurian Sea) (Fig. 2c-l) and the Amendolara Bank (Ionian Sea) (Fig. 6a, c, 7a, b). This facies is often characterized by the presence of ceriantharians, sabellid polychaetes (e.g., *Myxicola* sp.), sea stars, sea urchins [e.g., *Stylocidaris affinis* (Philippi, 1845)], holothurians and fishes [e.g., *Anthias anthias* (Linnaeus, 1758)].

About 28% of *D. cornigera* records occur as thanatocoenoses resulting widespread in the Mediterranean Sea and the NE Atlantic Ocean (Fig. 8a). These aggregations are represented by iii) thanatocoenoses together with dense meadows of living colonies (only observed on the flanks of the Occhiali Seamount, Ligurian Sea) (Fig. 8b), iv) thanatocoenoses with sparse living colonies (Fig. 8c), and v) thanatocoenoses without living colonies (Fig. 8d-g). Thanatofacies with and without living *Dendrophyllia* colonies mainly occur on soft bottoms (50%) and outcropping rocks (41%). They result common on horizontal bottoms (47%) or sea beds with moderate inclination (49%) (Fig. 7a, b). Thanatocoenoses on vertical substrate have been only reported from the steep overhangs of the

Linosa Trough and off Malta (Sicily Channel) (Freiwald et al., 2009, 2011). *Dendrophyllia* thanatocoenoses are characterized by the presence of the sponges *Hamacantha (Vomerula) falcula* (Bowerbank, 1874), *Haliclona* cf. *bioxeata*, and *Pachastrella monilifera* Schmidt, 1868, the gorgonian *Bebryce mollis* Philippi, 1842, the crustaceans *Munida* cf. *tenuimana*, and *Plesionika* spp., the brachiopods *M. truncata* and *Gryphus vitreus* (Born, 1778) and the fishes *A. anthias*, *C. ruber*, *Capros aper* (Linnaeus, 1758) and *H. dactylopterus*. Interestingly, dense aggregations of the crinoid *Leptometra phalangium* (Müller, 1841) have been reported from the thanatocoenoses on the Vercelli Seamount.

Overall, *D. cornigera* bathymetrical distribution ranges from 30 to 1200 m, with the majority of the records being placed between 150 and 380 m. The different facies created by this scleractinian, however, present slightly different bathymetrical distributions (Fig. 7c). The sparse living colonies mainly occur between 120 and 330 m depth, suggesting a current mesophotic-upper bathyal distribution. The dense meadows occur in a narrow mesophotic belt between 90 and 130 m depth. Finally, thanatofacies occur in a wider and deeper bathymetrical range between 190 and 440 m depth.

3.3.* Dendrophyllia cornigera *global abundance and size

The analysis of the large ROV archive of the Italian coast indicates that 90% of the *D. cornigera* records show an average density lower than 1.6 colonies m^{-2}, with some high-density areas in the Ligurian Sea, off Sardinia and the Ionian Sea (Fig. 9a). In the Ligurian Sea, average densities of 2.2-3.3 colonies m^{-2} are reported from the coast of Sanremo, Savona and from the Ulisse Seamount. Remarkable sites in this area are represented by the Occhiali Seamount (up to 25 living col. m^{-2} have been reported from the extended thanatocoenoses characterizing this site) and the Mantice Shoal (where *D. cornigera* reaches the highest average density value of 35 colonies m^{-2}, on soft bottoms). Along the coast of Sardinia, high maximum densities are reported from the sloping to sub-horizontal outcropping rocks of the Olbia and Posada canyons (NE Sardinia) and near the island of St. Pietro (SW Sardinia), with up to 28 colonies m^{-2} and 20 colonies m^{-2}, respectively. Finally, up to 24 colonies m^{-2} are reported on the soft bottoms surrounding the Amendolara Bank, in the Ionian Sea. Overall, significant differences in the average density have been observed among different substrates (Kruskal-Wallis, $H = 32.56$, $p < 0.001$), with distinctly higher values reported from soft bottoms (4.4 ± 0.9 colonies m^{-2}), and progressively lower densities characterizing outcropping rocks (0.8 ± 0.1 colonies m^{-2}), coralligenous rocks (0.4 ± 0.1 colonies m^{-2}), and dead cold-water corals (0.3 ± 0.2 colonies m^{-2}) (Fig. 9b, Tab. 3).

A total of 1572 *D. cornigera* colonies have been measured in the present study along the Italian coast. Results indicated an average height of 8.7 ± 0.1 cm for this species. Significant differences in *D.*

cornigera average size have been observed for colonies growing on different substrates (Kruskal-Wallis, H = 25.96, $p < 0.001$). Colonies growing on soft bottoms (8.3 ± 0.2 cm) results significant smaller than those growing on outcropping rocks (9.4 ± 0.2 cm), but larger than those growing on coralligenous rocks (6.8 ± 0.5 cm) (Fig. 9c, Tab. 3). The highest average size (11.9 ± 2.1 cm) has been reported for the colonies growing on dead cold-water corals, where the maximum size of 41.8 cm has also been recorded, but the Dunn's *post-hoc* test indicates that this latter difference is not significative.

The size-class frequency distribution (Fig. 9d), calculated separately for each substrate type, indicates a unimodal, almost overlapping distribution for *Dendrophyllia* colonies growing on soft bottoms and outcropping rocks, with the size class 5 – 10 cm being the most common. A unimodal distribution is also reported for colonies settled on coralligenous rocks, but in this case, the most representative class is the smaller one (0 – 5 cm). A more irregular size-class frequency distribution is showed by the colonies growing on dead cold-water coral remains, with one major peak in the smallest class (0 – 5 cm) and a second, less pronounced peak in the 25 – 30 cm class, indicating the presence of large specimens.

3.4. Ageing **Dendrophyllia** *thanatocoenoses*

Conventional and calibrated radiocarbon ages carried out on the five samples of *D. cornigera* are reported in Table 2. The estimated ages of the analyzed coral branches range between 399 and 13060 years before present (1950), with the oldest sample occurring from the Vercelli Seamount (Tyrrhenian Sea).

4. Discussion

4.1. **D. cornigera,** *a largely adaptable species*

The present study provides a detailed characterization of the ecological settings of *Dendrophyllia cornigera*, presenting the largest dataset ever assembled for this species (383 records) covering its whole geographical range. Information on substrate type, inclination and facies resulted scarcely reported in the literature, but additional information has been extrapolated from pictures and drawings associated with the publications. Furthermore, the inclusion of the large ROV dataset (made of 142 *D. cornigera* records along the Italian deep continental shelf, slope and seamounts) allowed to increase the robustness of the dataset.

The wider adaptability of this species with respect to other cold-water corals has been already highlighted by several authors, especially regarding its broad bathymetrical distribution, thermal and turbidity tolerance (Roberts et al., 2006; Naumann et al., 2013; Gori et al., 2014; Castellan et al., 2019; Reynaud and Ferrier-Pagès, 2019; Reynaud et al., 2021). The results of the present study clearly depict a large suitability of this species to a wide combination of environmental constraints, including depth (from the upper circalittoral to the lower bathyal plains), substrate inclination (from horizontal to vertical) and substrate type (including hard and soft bottoms). This plasticity allows *D. cornigera* to participate in different benthic communities, including those dominated by sponges (Bo et al., 2012), gorgonians (Fig. 2a), black corals, and deep-sea scleractinians (Fig. 5d), and to create its own, both on hard and soft bottoms.

4.2. Living populations on hardgrounds

It is not surprising that the majority of *Dendrophyllia* records (83%) were reported from hardgrounds. Indeed, several studies report *D. cornigera* as a typical hard bottom species (e. g., Hebbeln et al., 2009; Orejas, 2009; Altuna and Poliseno, 2019; Chimienti et al., 2019). In this case, *D. cornigera* falls in various habitat categories of the updated classification of marine benthic habitat types for the Mediterranean Sea (SPA/RAC-UN Environment/MAP, 2019; Montefalcone et al., 2021), namely MD1.515, MD1.53, ME1.515, regarding the offshore circalittoral and upper bathyal hardgrounds.

Considered hardgrounds are generally represented by outcropping rocks, both in the Mediterranean Sea and the Atlantic Ocean. The average density values here calculated on the Italian outcropping rocks (0.8 colonies m^{-2}) are similar to those reported in other studies: for example, an average of 0.5 colonies m^{-2} have been reported from the Cantabrian Sea (Sanchez et al., 2009). Distinctly lower average density characterizes the *D. cornigera* population of Cap de Creus, in the NW Mediterranean Sea, where 0.01 colonies m^{-2} are reported (Orejas et al., 2009). Low densities of *D. cornigera* are common as this species is not known to create structured coral reefs; nonetheless, high-density patches are occasionally observed on hardgrounds, with up to 11 colonies m^{-2} reported from the Cantabrian Sea (Sanchez et al., 2009) and 28 colonies m^{-2} from the Posada Canyon (NE Sardinia) (present study).

On coralligenous rocks, *D. cornigera* results widely distributed in the Mediterranean Sea, in particular in the Tyrrhenian Sea, especially from offshore banks, islands and seamounts or coastal areas characterized by transparent water, allowing for deeper penetration of light and coralline algae growth. This association is easily explainable by the overlapping of the shallower records of *D. cornigera* with the lower bathymetrical limit of coralline algae. The low density and the small size of *D. cornigera* on coralligenous rocks (Fig. 9b-d) also support the hypothesis that these records represent the upper bathymetrical limit of this species. Records of *D. cornigera* on maërl beds are rare (Vafidis, 1997), as well as other records on coralligenous rocks outside the Mediterranean Sea (Moseley, 1881).

D. cornigera has often been reported associated with the white corals *Lophelia pertusa* and *Madrepora oculata*. In the Mediterranean Sea, these biocoenoses results widely distributed along canyons and seamounts. Eight main white coral provinces, characterized by a lush growth of structuring scleractinians, have been identified so far (Angeletti et al., 2020). *D. cornigera* has been reported from all the Mediterranean white coral provinces, but not always directly growing on the coral frameworks. Indeed, *D. cornigera* has only been reported growing on outcropping rocks in the Strait of Sicily and the Gulf of Lions provinces. In addition, *D. cornigera* growing on *Madrepora*/*Lophelia* remains has been reported from the Grande Vasière Bank (Bay of Biscay) and off the Atlantic coast of Morocco (Le Danois, 1948; Wienberg et al., 2009), indicating that this association also occurs in the NE Atlantic Ocean. The large size reached by some colonies settled on dead cold-water scleractinians (Fig. 9c, d), supports the high stability of this environment with respect to shallower ones.

4.3. Living populations on soft bottoms

The wide occurrence of *D. cornigera* on soft bottoms, both in the NE Atlantic Ocean and the Mediterranean Sea (Fig. 6), represents one of the most interesting outcomes of this study. Literature review and ROV archive analyses indicated that 17% of the records occur on silted detritic bottoms. The wide occurrence of this species on non-cohesive seafloor and the existence of at least two high-density populations, support the existence of a proper *D. cornigera* facies developing on this substrate. A distinct megabenthic community dominated by *D. cornigera* indeed emerged from the community analysis carried out on the Ligurian deep continental shelf and shelf-break (Enrichetti et al., 2019). Given their extension and structuring function, dense meadows of dendrophylliids on soft bottoms in offshore circalittoral environments should be included in a distinct habitat category, as already suggested by Michez et al. (2014), reporting detritic bottoms with dead coral fragments and living colonies of *D. cornigera* from French and western Corse canyons. Currently, however, the most updated classification of marine benthic habitat types for the Mediterranean Sea (SPA/RAC-UN Environment/MAP, 2019; Montefalcone et al., 2021), only presents a “Facies with Scleractinia” for the upper bathyal sands (ME5.518) and muds (ME6.514), without any reference to these dendrophylliids.

The density estimation for this facies may shows differences depending on the methodological approach employed to calculate the areas (point-like still frame method vs QGIS track surface method), however abundance values are always considerably high. Soft bottom high-density facies have been reported only from two deep Mediterranean shoals, namely Mantice Shoal and Amendolara Bank, suggesting peculiar characteristics of these sites. Both shoals are located at the edge between the deep circalittoral and the upper bathyal, mainly at mesophotic depths. These shoals are surrounded by detritic soft bottoms and are characterized by high levels of siltation (Bo et al., 2012). Several topographic and oceanographic features support the development of rich megabenthic communities on the Mantice Shoal, including the upwelling of deep water through the nearby canyons and the occurrence of anti-cyclonic mesoscale and sub-mesoscale eddies (Cattaneo-Vietti et al., 2010; Casella et al., 2011; Bo et al., 2014a; Enrichetti et al., 2019). These characteristics may explain the large extension of the populations and the high-density values reported, at least from the Mantice Shoal. The analysis of the video transects allows to estimate that the sole North-eastern *Dendrophyllia* meadow of the Mantice Shoal described here (Fig. 1c, 3c) occupies an area of approximately 0.8 hectares, hosting nearly 33500 colonies and representing by far the largest population of this species ever described. Furthermore, it has to be considered that, around the shoal, there are unexplored areas with suitable depth and substrate which might host additional patches.

D. cornigera is not the only dendrophylliid known to form facies on soft bottom. Indeed, the congeneric *D. ramea*, forms dense aggregations on sandy bottoms off Cyprus (Orejas et al., 2019b) and in the Ionian Sea (Korinthiakos Gulf, Greece) (Salomidi et al., 2010), thus indicating that the affinity for the soft bottoms could be a characteristic of the whole genus *Dendrophyllia*.

The formation of these aggregations on soft bottoms is probably linked to the ability of *Dendrophyllia* larvae to settle on small hard substrates, probably represented by small pebbles, shell fragments, or other carbonatic skeletons remains. It is plausible that aggregations nearby rocky reliefs receive inputs also from the detachment of *Dendrophyllia* colonies or branches from sloping or vertical hardgrounds, which accumulate on the surrounding areas and partially survive. Within these beds, *Dendrophyllia* colonies usually lie in a natural upright position, but the high instability of the soft bottom may induce large colonies to overturn, limiting the maximum size reached by the colonies with respect to those growing on the outcropping rocks (Fig. 9c). A similar effect of the substrate instability on the growth of structuring anthozoans has been reported from *Paramuricea macrospina* (von Koch, 1882) on the maërl beds of the Menorca Channel (Gori et al., 2017). The instability of the soft bottoms can also partially explain the occurrence of numerous dead colonies, allowing to exclude the direct mechanical impact of fishing gears among the causes of death, despite numerous lines have been often reported entangling *D. cornigera* colonies on the Mantice Shoal hardgrounds (Bo et al., 2014a). The presence of a population of free-living colonies in this area can be certainly related to the absence of trawling activities due to the vicinity of the Savona harbor and the complex topography of the Vado Canyon. In addition, it has been demonstrated that dendrophylliid corals display regenerative ability and high survival rates, independently from food availability or fragment size (Luz et al., 2021).

4.4. **D. cornigera** ***thanatocoenoses***

Dendrophyllia cornigera thanatocoenoses result common at bathyal depth in the NE Atlantic Ocean and Mediterranean Sea (Fig. 8a), ultimately supporting the creation of the category "Thanatocoenosis of corals, or Brachiopoda, or Bivalvia, or sponges" (MD2.52, ME2.52) in the updated SPA/RAC-UNEP/MAP classification scheme of marine benthic habitats (Fourt Goujard, 2012; SPA/RAC–UN Environment/MAP, 2019; Montefalcone et al., 2021).

Dendrophyllia thanatocoenoses are common on soft bottoms but can also occur on hard grounds. In some cases, the coral rubble extends over considerable areas, as along the Moroccan Atlantic coast, where an approximately 100 m-wide belt of *Dendrophyllia* remains extends from Rabat to Agadir (Zibrowius, 1981). More often, the coral rubble does not form continuous belts, resulting mainly localized in build-ups or coral mounds, as on the Beta Mound (Pen Duick Escarpment, Gulf of Cadiz) (De Mol et al., 2012). In the Mediterranean Sea, important thanatocoenoses occur in the Alboran, Ligurian, Tyrrhenian, and Aegean seas, and along the Strait of Sicily. In the Alboran region, thanatocoenoses result common, and a mound formation unit dominated by dendrophylliids remains has been reported from the Cabliers Coral Mound Province (Corbera et al., 2021). In the Ligurian Sea, *Dendrophyllia* thanatocoenoses are generally associated with lower mesophotic and upper bathyal canyons (Fourt and Goujard, 2012) and seamount tops (Ulisse, Penelope, Santa Lucia) (Bo et al., 2021) and often co-occur with living colonies, especially on the Occhiali Seamount, where a dense meadow develops on the dead branches (Fig. 8b). *Dendrophyllia* thanatocoenoses result widespread also in the Tyrrhenian Sea, where they develop on continental slopes, canyons and seamounts. Particular interesting is the cases of the Corse Channel, where a mound of *Dendrophyllia* rubble hosts a CWC reef dominated by large colonies of *Madrepora oculata* (Fig. 8f) (Angeletti et al., 2020). On the Vercelli Seamount, a wide belt of *Dendrophyllia* rubble with sparse living colonies encircles the summit pinnacle, at about 180-200 m depth (Bo et al., 2010). Finally, dense patchy accumulations of *Dendrophyllia* remains also occur from the Lampedusa Bank (Strait of Sicily) and off San Vito (NE Sicily) (Bo et al., 2014b). Similarly to the dense living meadows, the thanatocoenoses on soft bottoms, with colonies in place, represent an indirect indicator of low trawling effort. The patchy accumulations of coral rubble observed in the Sicily Channel, an area heavily impacted by trawlers (Ferrà et al., 2020), suggest that coral debris could be moved and amassed, often at the base of rocky reliefs, as shown in Fig. 8g.

Radiocarbon dating data of dendrophylliid corals are scarce in the literature (Schröder-Ritzrau et al., 2005). Several authors consider the majority of these thanatocoenoses dating back to the Late Pleistocene (126 – 12 ka) (Blanc et al., 1959; Zibrowius, 1980; Vertino et al., 2014, 2019), supporting a greater development of *D. cornigera* in the recent geological past. Indeed, dendrophylliid-dominated facies have been recorded from the Miocene and Early Pleistocene (back to 23 MYA) (Bosellini et al., 1999; Mastandrea et al., 2002), when the diversity of dendrophylliid corals in the Mediterranean Sea was remarkably higher (Vertino et al., 2014, 2019). Dendrophylliid diversity and distribution considerably decreased during the Pleistocene, when important paleo-climatic fluctuations such as glacial-interglacial cycles caused drastic changes in relative sea-level, seawater temperature, circulation patterns, and many other environmental variables, including surface productivity, siltation, water oxygenation and sapropel deposition events (Dorschel et al., 2005; Roberts et al., 2006; Fink et al., 2012, 2015; Thierens et al., 2013; Benjamin et al., 2017).

Most of the coral samples analyzed in the present study range between 5000 and 400 YBP (Holocene), with only one sample from the Vercelli Seamount being placed at the boundary between Pleistocene/Holocene (13060 YBP), and therefore representing the only one whose death can be related to the Late Pleistocene climate fluctuations. These results suggest that the most recent thanatocoenoses were not related to large-scale geological and oceanographical events, including the Holocene sapropel S1, which occurred about 10500-6000 YBP.

In addition, the current distribution of the soft-bottom thanatocoenoses in the upper bathyal indicates that before the Pleistocene/Holocene boundary and the sea level rise, these facies (now dead) constituted living dense meadows in shallower mesophotic waters, as observed today around the Mantice Shoal and Amendolara Bank. For example, the thanatocoenosis of the Vercelli Seamount (now at about 180-200 m depth) was located at about 120-140 m depth. Taphonomic processes, and particularly silting conditions, certainly play a major role in preserving the dead branches and determining the amount of the coral rubble accumulated. We may also hypothesize that, in the past, *D. cornigera* dense living meadows on soft bottoms were probably more common.

5. Conclusions

Dendrophyllia cornigera represents an important structuring scleractinian in the Mediterranean Sea for many thousands of years. Its great adaptability in terms of environmental settings allows this species to tolerate temperature and turbidity variations, and its ability to settle on both hard and soft bottoms led to the creation of different facies on a wide bathymetrical range. Indeed, it participates in typical offshore circalittoral biocenoses as well as upper bathyal environments. Its branched colonies can reach considerable size, supporting its role as a structuring species. Furthermore, its dead branches can create a secondary complex habitat that attracts a rich community of associated species, including fishes and invertebrates. The inclusion of these facies in the most updated habitat classification schemes represents an essential action toward the conservation of a species considered "Endangered" by the IUCN Red Lists.

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Supplementary materials

SM1. ROV video showing the *Dendrophyllia cornigera* meadow of the Mantice Shoal. Lasers distance: 8 cm

SM2. Summary of the information on *Dendrophyllia cornigera* extracted from the bibliographic research and the new data presented in this study.

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Fig. 2. ROV images of the Mantice Shoal. *Dendrophyllia cornigera* on hard bottoms (a-b). Sparse colonies associated with forests of the gorgonian *Eunicella cavolini* (*Ec*) (a) and (b) on bare rocks with encrusting sponges (Es), solitary scleractinians (Ss), and echinoderms (Cid, *Stylocidaris affinis*; H, *Holothuria* sp.). *Am*, *Astrospartus mediterraneus*; *Ax*, *Axinella* sp.; *Pc*, *Paralcyonium coralloides*. *D. cornigera* meadow on soft bottoms (c-l). Wide views (c, l) and close-ups (d-k). Associated fauna includes cidarid sea urchins (Cid) (d, g), the hermit crab *Dardanus arrosor* (*Da*) (e), serpulids (Ser) (e, l), encrusting sponges (Es), small colonies of *E. cavolini* (*Ec*) (g), the sabellid *Myxicola* sp. (*Mi*), and the fishes *Lappanella fasciata* (*Lf*) (j), *Ophisurus serpens* (k) and *Pagellus erythrinus* (*Pe*). Unlabeled arrows in (e-g) and images (h) and (i) indicate overturned or broken colonies reorganizing polyps' orientation. Scale bar: 10 cm.

Fig. 3. Characteristics of the *Dendrophyllia cornigera* meadow of the Mantice Shoal. (a) Terrain profiles of the Mantice Shoal showing the occurrence of *D. cornigera* aggregations. Inset: multibeam map showing the spatial location of the two terrain profiles AB and CD displayed in (a); see Table 1 for patches numeration. (b) Size-class frequency distribution of *D. cornigera* population of the Mantice Shoal. (c) Multibeam map of the NE sector of the Mantice Shoal showing the possible extension of the *Dendrophyllia* meadow traced by considering suitable substrate, inclination and depth (red dashed line).

Fig. 4. *Dendrophyllia cornigera* geographical distribution. Map of the NE Atlantic Ocean and the Mediterranean Sea showing all the *D. cornigera* records included in the present study. Inset: global map including *D. cornigera* records from the Indo-Pacific.

Fig. 5. *Dendrophyllia cornigera* substrate type. (a) Map of the NE Atlantic Ocean and the Mediterranean Sea showing the distribution of *D. cornigera* records according to its substrate. ROV images of *D. cornigera* settled on outcropping rock (b) (Off Gioiosa, NE Sicily, 190 m), coralligenous rock (c) (Capo Teulada, South-western Sardinia, 120 m), cold-water coral frameworks (d) (Corsica Channel, 408 m), and soft bottoms (e) (Palinuro Seamount, 180 m).

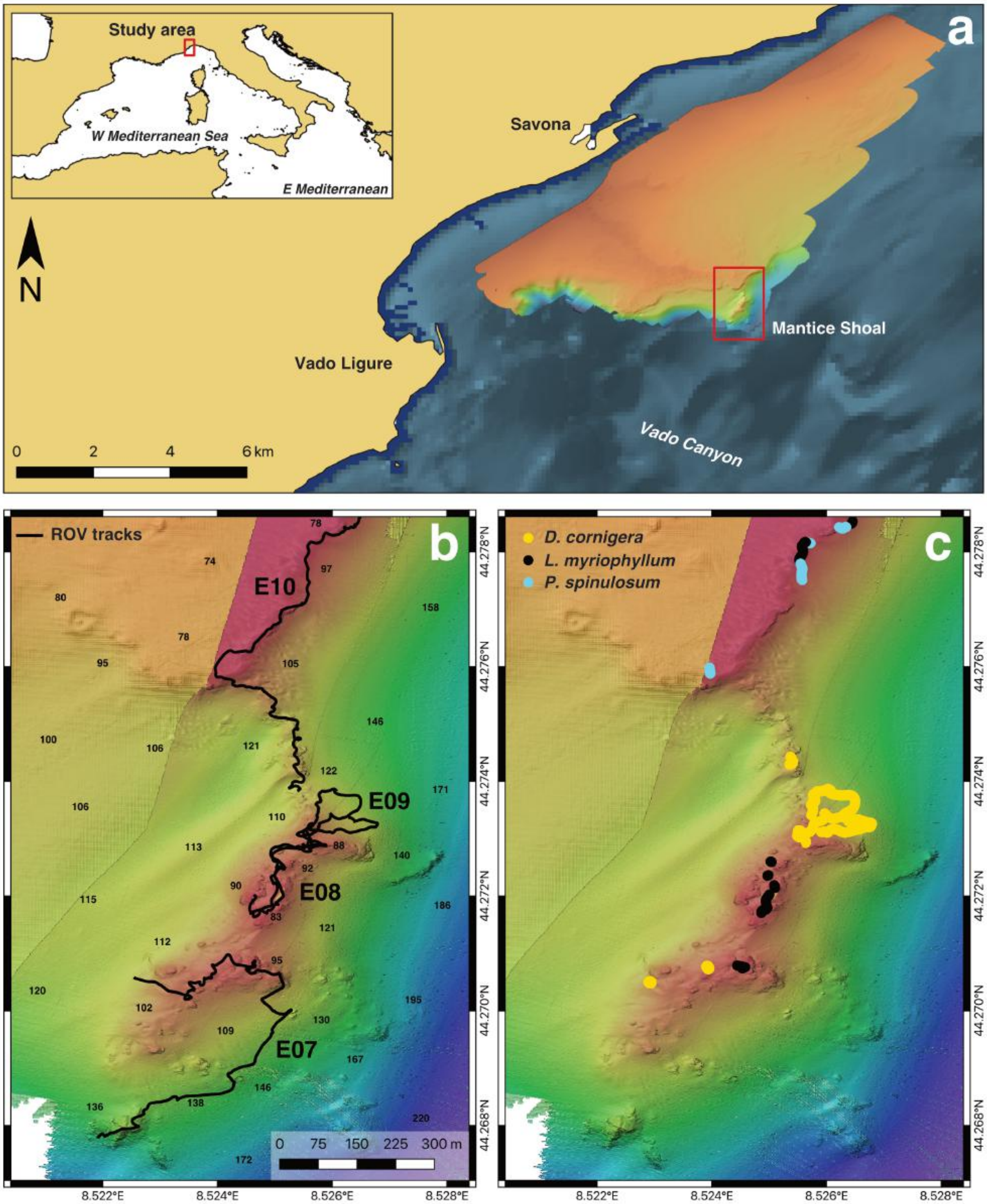
Fig. 6. Living facies of *Dendrophyllia cornigera*. (a) Map of the NE Atlantic Ocean and the Mediterranean Sea showing the distribution of the living facies of *D. cornigera*. Within these facies, *Dendrophyllia* colonies can occur as sparse and isolated as in (b) (Bordighera Canyon, Ligurian Sea, 165 m), or dense populations, as in the cases of the Maledetti Shoal or (c) the Amendolara Bank (125 m).

Fig. 7. Ecological characteristics of *Dendrophyllia cornigera* facies. Three main facies dominated by *D. cornigera* have been identified: sparse living colonies (SLC), dense meadows (DM), and thanatocoenoses (TAN). These facies present different preferences in substrate type (a), inclination (b), and depth (c). OR: outcropping rocks; CR: coralligenous rocks; dCWC: dead cold-water corals; SB: soft bottoms; Hor: horizontal; Slo: sloping; Ver: vertical.

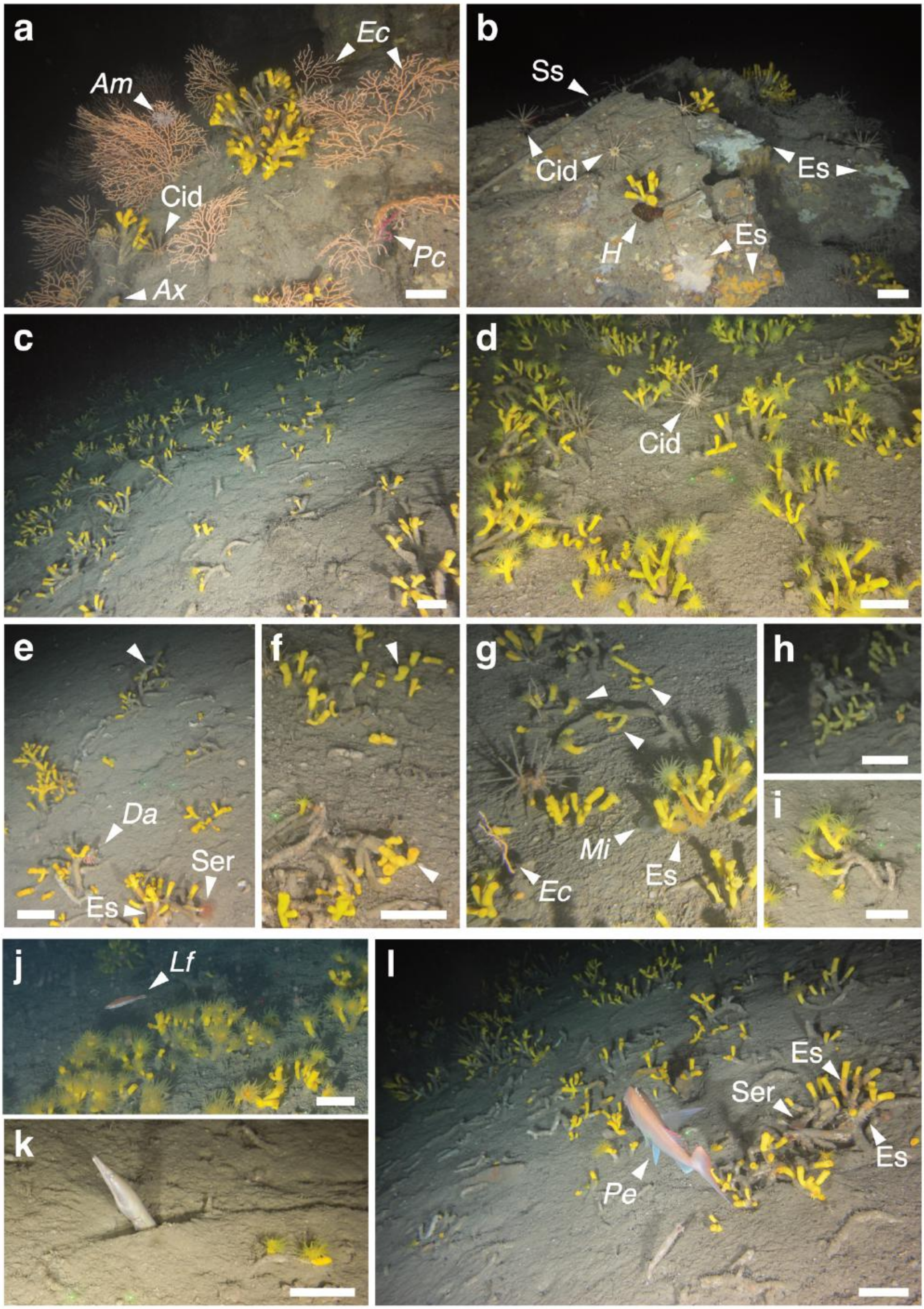
Fig. 8. Thanatofacies of *Dendrophyllia cornigera*. (a) Map of the NE Atlantic Ocean and the Mediterranean Sea showing the distribution of the thanatofacies of *D. cornigera*. The large thanatocoenosis of the Occhiali Seamount (b) (310 m) hosts a dense meadow of living colonies. More

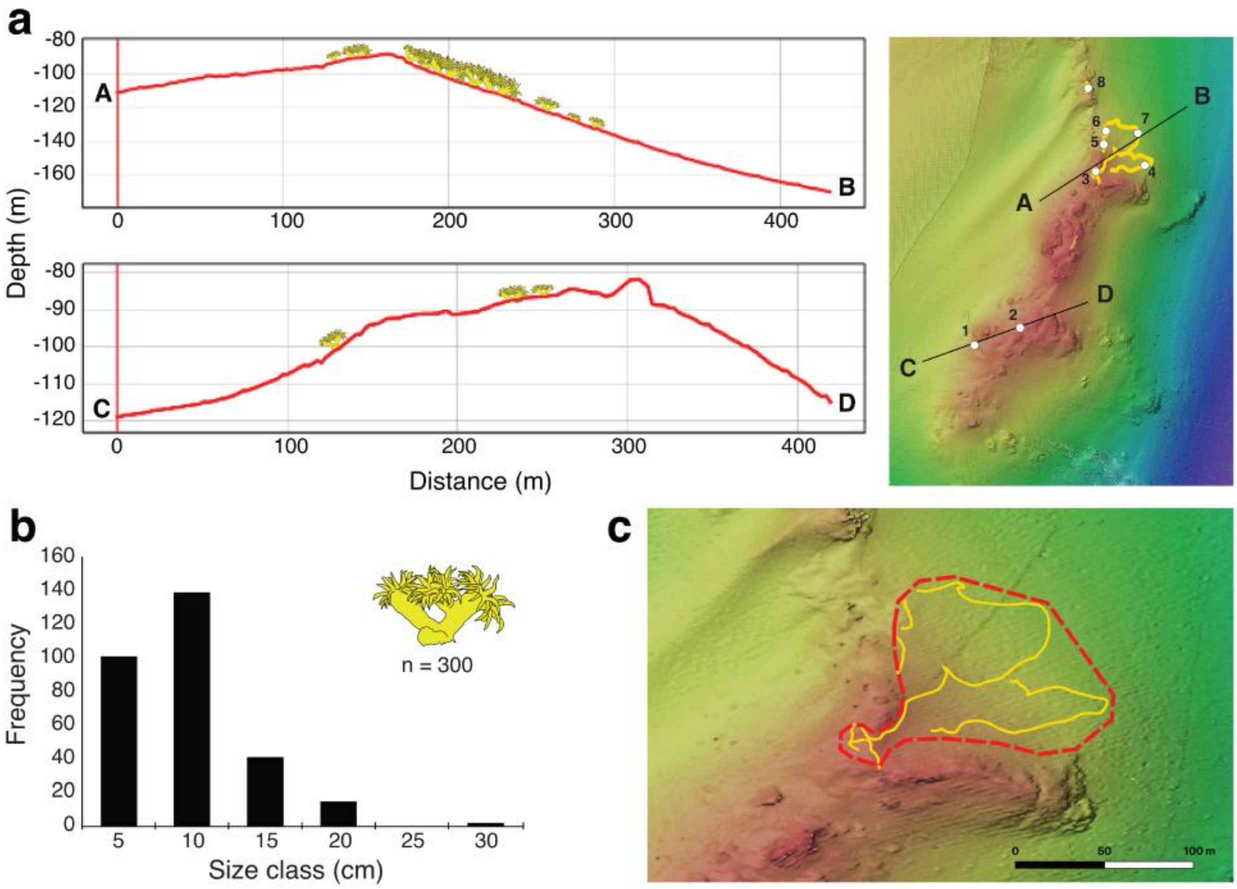
often, only few living colonies are present, as in the case of the Palinuro Seamount (c) (180 m), or they result completely absent (d-g). (d) Vercelli Seamount, 200 m. (e) Off San Vito, NE Sicily, 260 m. (f) *D. cornigera* rubble forms a large mound that supports the growth of a living *Madrepora oculata* framework (Corsica Channel, 440). (g) *Dendrophyllia* rubble accumulation nearby the Graham Bank (Sicily Channel, 180 m).

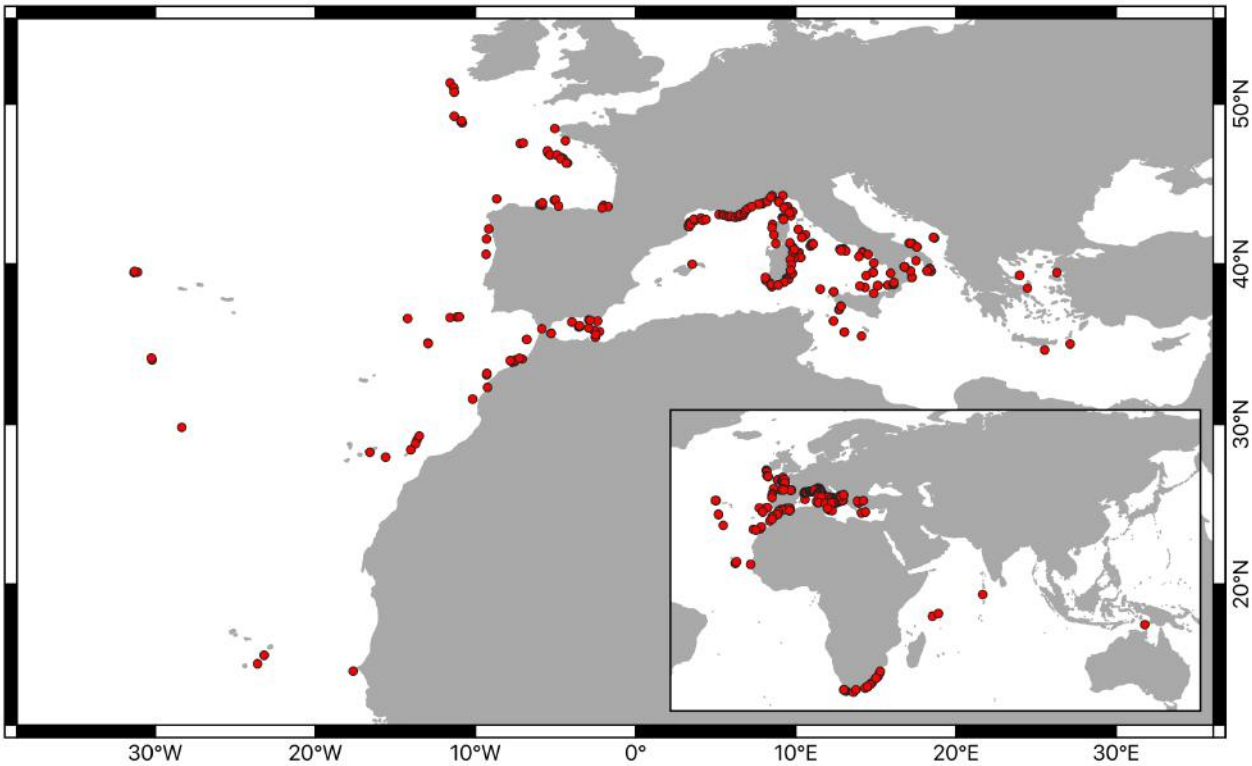
Fig. 9. *Dendrophyllia cornigera* density and morphometry. (a) Distribution of *D. cornigera* records along the Italian coast according to average density values. Average density (b) and average size (c) of *D. cornigera* according to four different substrate types. Size-class frequency distribution (d) of *D. cornigera* according to four different substrate types. SB: soft bottoms; OR: outcropping rocks; CR: coralligenous rocks; dCWC: dead cold-water corals.

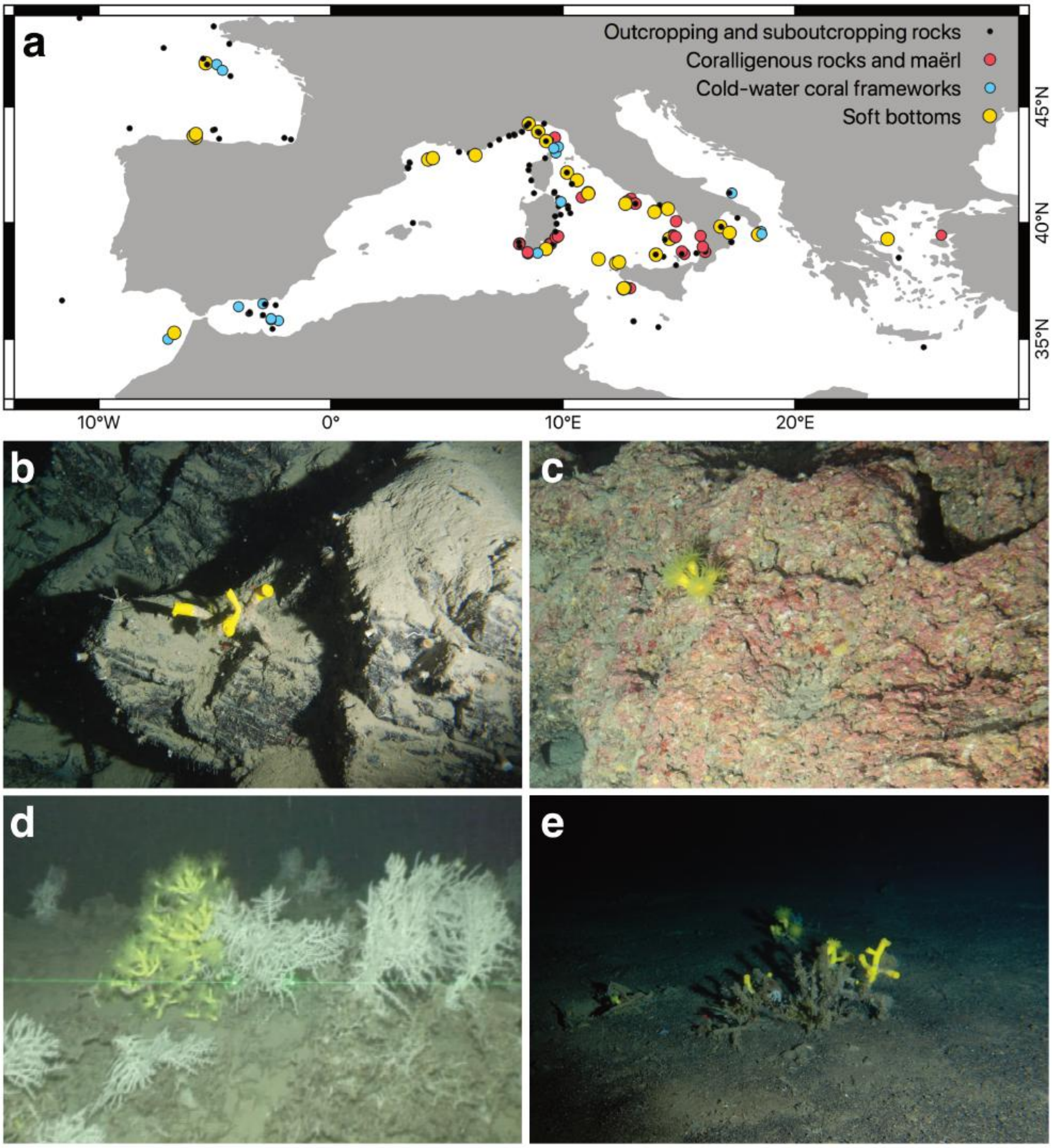


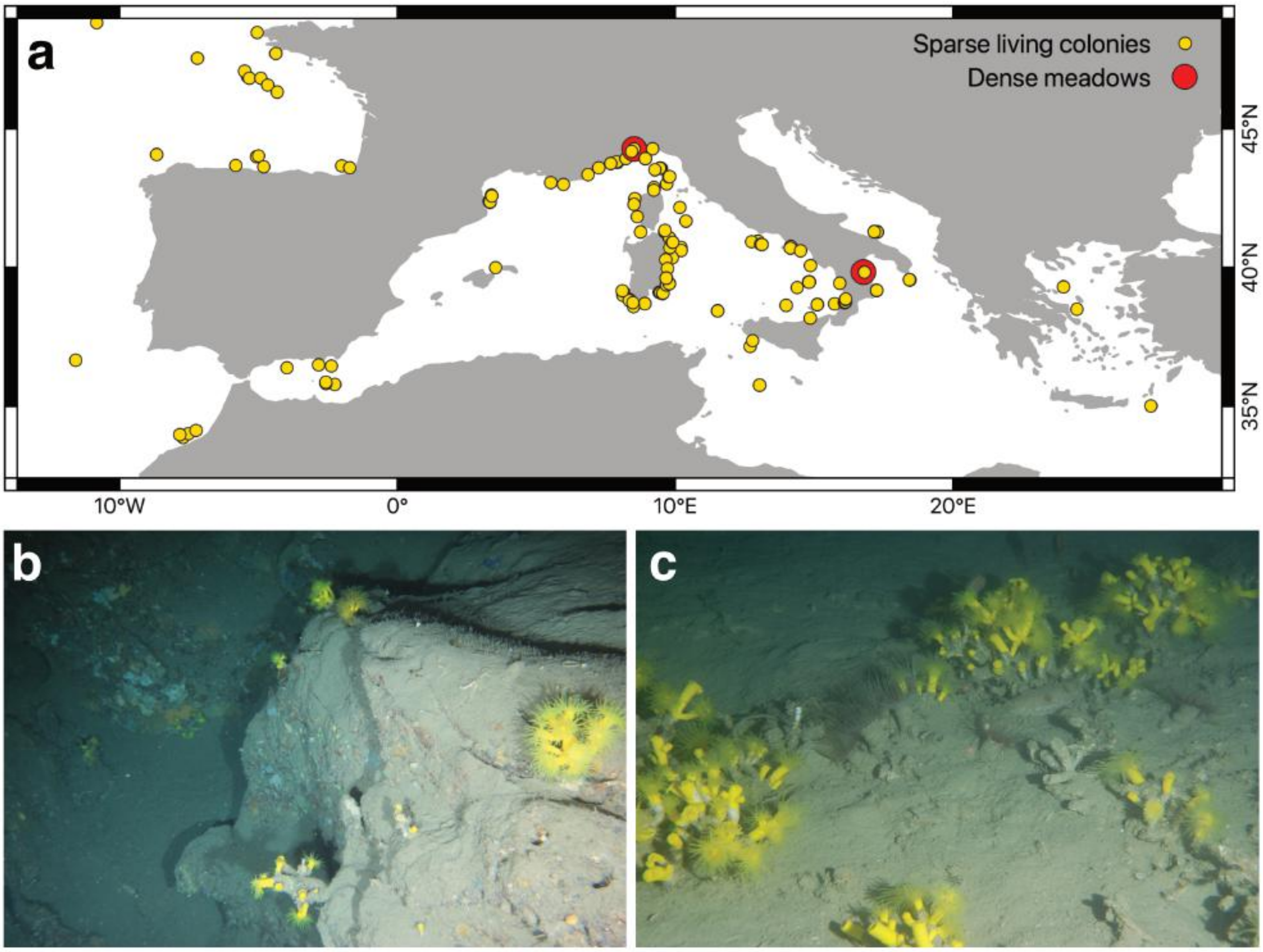
a
Study area
W Mediterranean Sea
E Mediterranean
N
Savona
Mantice Shoal
Vado Ligure
Vado Canyon
0 2 4 6 km
b
ROV tracks
E10
E09
E08
E07
0 75 150 225 300 m
c
D. cornigera
L. myriophyllum
P. spinulosum
44.278°N
44.276°N
44.274°N
44.272°N
44.270°N
44.268°N
8.522°E
8.524°E
8.526°E
8.528°E

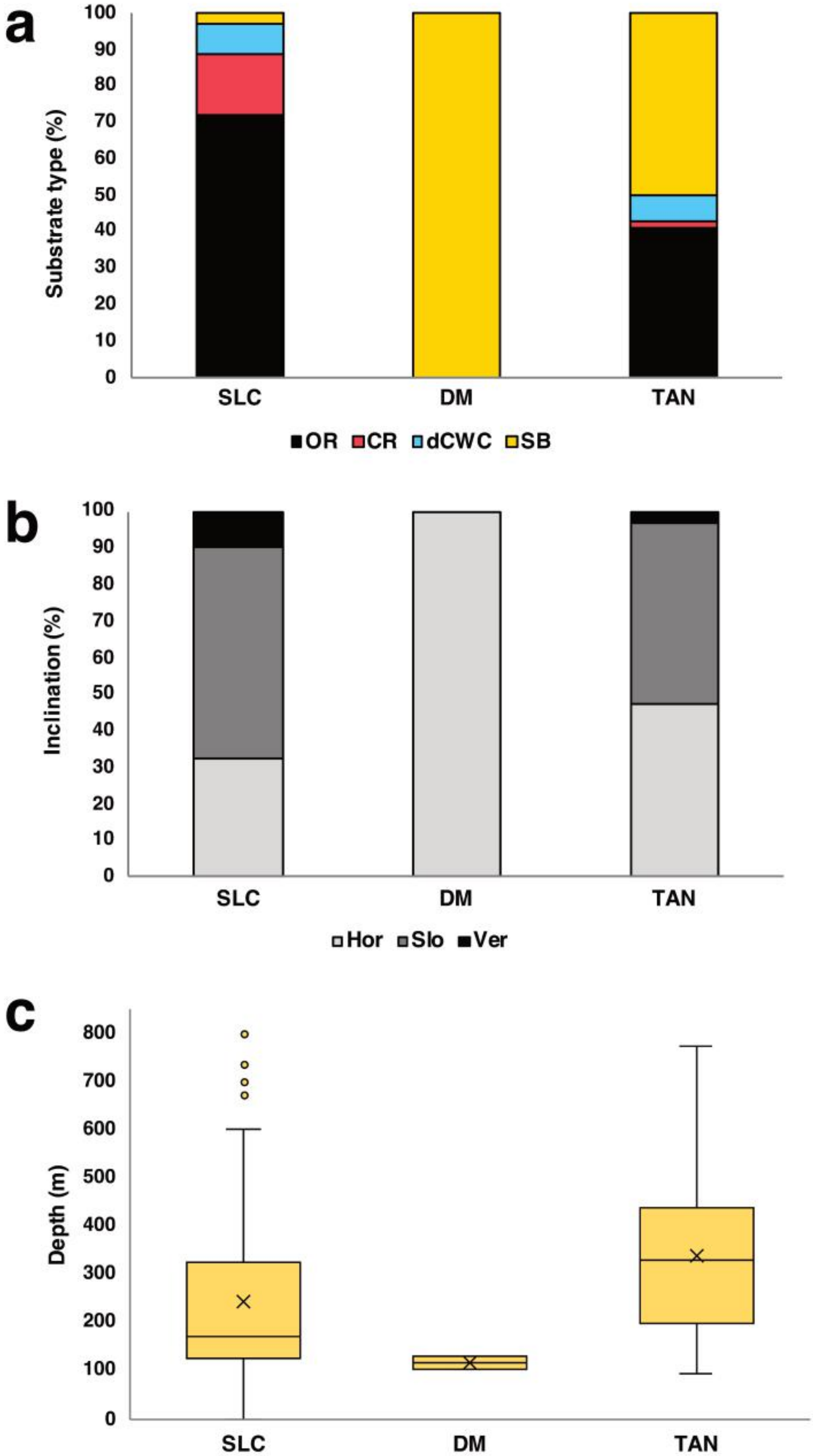

a
Am
Ec
Cid
Pc
Ax
b
Ss
Cid
Es
H
Es
c
d
Cid
e
Da
Ser
Es
f
g
Mi
Ec
Es
h
i
j
Lf
k
l
Es
Ser
Es
Pe

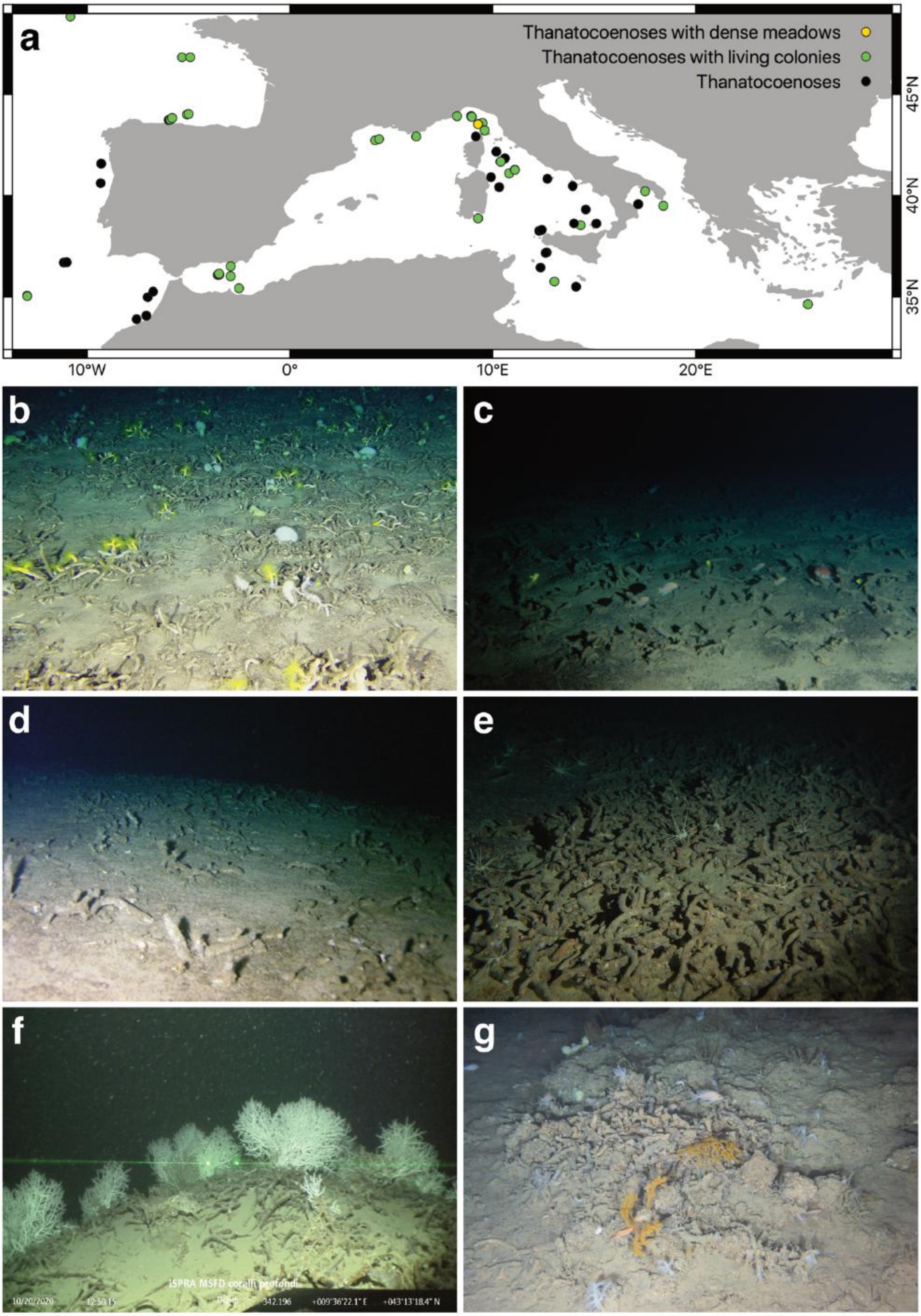

a
Depth (m)
Distance (m)
A
B
C
D
-80
-100
-120
-140
-160
-90
-110
0
100
200
300
400
1
2
3
4
5
6
7
8
b
Frequency
Size class (cm)
n = 300
0
20
40
60
80
100
120
140
160
5
10
15
20
25
30
c
0
50
100 m

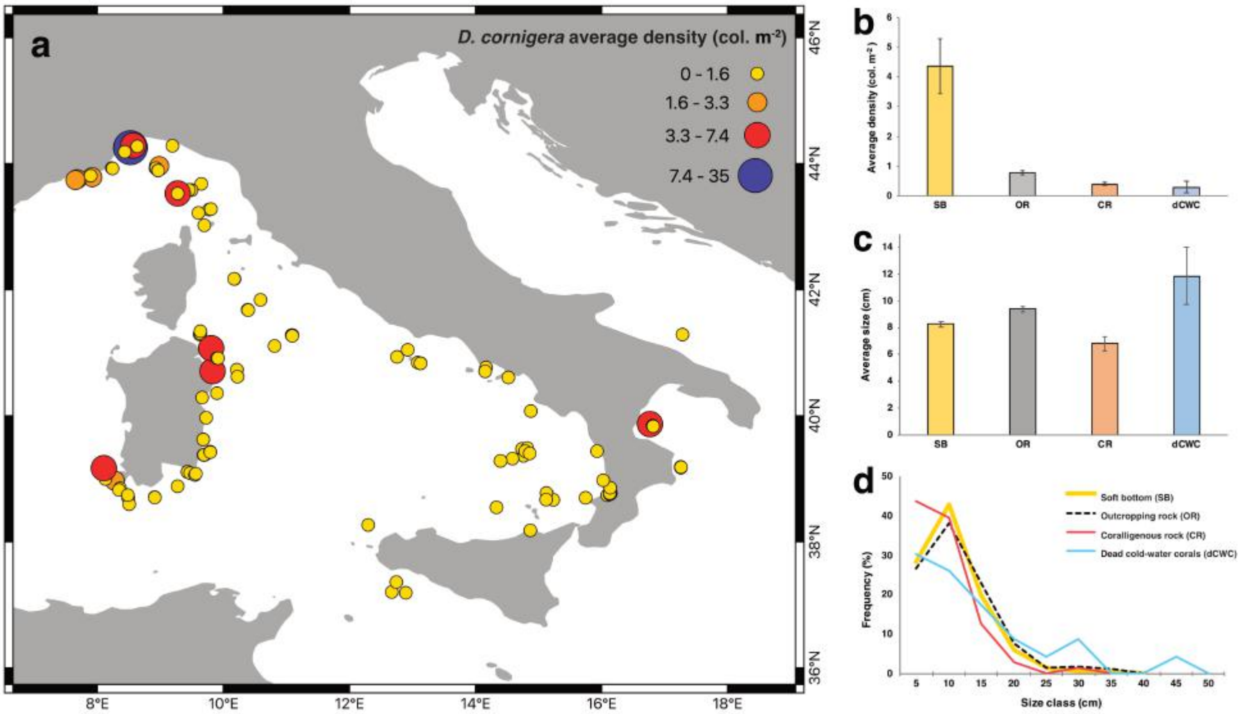

50°N
40°N
30°N
20°N
30°W
20°W
10°W
0°
10°E
20°E
30°E


a
Outcropping and suboutcropping rocks
Coralligenous rocks and maërl
Cold-water coral frameworks
Soft bottoms
45°N
40°N
35°N
10°W
0°
10°E
20°E
b
c
d
e


a
Sparse living colonies
Dense meadows
45°N
40°N
35°N
10°W
0°
10°E
20°E
b
c


a
Substrate type (%)
100
90
80
70
60
50
40
30
20
10
0
SLC
DM
TAN
OR
CR
dCWC
SB
b
Inclination (%)
100
90
80
70
60
50
40
30
20
10
0
SLC
DM
TAN
Hor
Slo
Ver
c
Depth (m)
800
700
600
500
400
300
200
100
0
SLC
DM
TAN


a
Thanatocoenoses with dense meadows
Thanatocoenoses with living colonies
Thanatocoenoses
45°N
40°N
35°N
10°W
0°
10°E
20°E
b
c
d
e
f
ISPRA MSFD coralli profondi
10/20/2020
12:50:15
342.196
+009°36'22.1" E
+043°13'18.4" N
g


a
D. cornigera average density (col. m⁻²)
0 - 1.6
1.6 - 3.3
3.3 - 7.4
7.4 - 35
8°E
10°E
12°E
14°E
16°E
18°E
36°N
38°N
40°N
42°N
44°N
46°N
b
Average density (col. m⁻²)
SB
OR
CR
dCWC
c
Average size (cm)
SB
OR
CR
dCWC
d
Soft bottom (SB)
Outcropping rock (OR)
Coralligenous rock (CR)
Dead cold-water corals (dCWC)
Frequency (%)
Size class (cm)