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Basin-scale occurrence and distribution of mesophotic and upper bathyal red coral forests along the Italian coasts

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Abstract

The analysis of 879 ROV dives carried out along the Italian coasts on hard substrata at mesophotic and upper bathyal depths (40-775 m) allowed us to evaluate the current basin-scale presence, relative abundance, bathymetric limits, and habitat preferences of one of the most charismatic Mediterranean habitat-former anthozoan species, *Corallium rubrum* (Linnaeus, 1758). The species is widespread, and its occurrence ranged from 13% of the explored sites in Ionian Calabria to a hotspot of approximately 80% in Sardinia. Population relative densities were generally low (< 10 colonies m^{-2}), except along the Sardinian coasts and in some areas along the Apulian coast. Almost no red coral colonies were observed between 60 m and 590 m in the nine explored offshore seamounts in the Ligurian and Tyrrhenian Seas. A distinctive coastal distribution discontinuity was found in the Ionian Sea. The optimum bathymetric distribution was between 75 m and 125 m, and no colonies were found below 247 m. Red coral colonies showed a preference for biogenic habitats dominated by crustose coralline algae (CCA) and vertical substrata. The species was absent on iron wrecks. *Corallium rubrum* disappeared from 14% of the historical fishing banks, while it was confirmed in 86% of them, some of which have been deeply harvested in the past. In particular, the still flourishing Sardinian populations could be supported by the high reproductive potential and favourable hydrodynamic conditions in the area.

Keywords: *Corallium rubrum*; Mediterranean Sea; relative abundance; habitat preferences; historical fishing banks.

Introduction

In the Mediterranean Sea, the precious red coral *Corallium rubrum* (Linnaeus, 1758) is a charismatic species of great commercial and naturalistic value (Cicogna & Cattaneo-Vietti, 1993; Cicogna *et al*., 1999; Garrabou & Harmelin, 2002; Tsounis *et al*., 2007, 2010; Santangelo *et al*., 2007; Dounas *et al.*, 2009; Cattaneo-Vietti & Bavestrello, 2010; Santangelo & Bramanti, 2010; Bramanti *et al*., 2014; Garrabou *et al*., 2017; Cannas *et al*., 2019). Its populations are known to develop on steep walls, overhangs, outcrops, small cavities, and sublittoral caves between the infralittoral and circalittoral zones of the basin. Isolated colonies are also found at greater depths, down to 1,016 m around the Maltese Archipelago (Taviani *et al*., 2010; Costantini *et al*., 2010; Knittweis *et al*., 2016).

Red coral shows a broad geographic pattern of distribution, occurring in the western Mediterranean Sea and adjacent Atlantic coasts, such as those of Morocco, SW Portugal, Cabo Verde, and in some areas of the Adriatic, Ionian and Aegean seas (Zibrowius, 1980; Zibrowius *et al*., 1984; Dounas *et al.*, 2009; Boavida *et al*., 2016; Cannas *et al*., 2019).

The species characterises one of the most representative facies among those belonging to coralligenous habitats (Pérès & Picard, 1964; Ballesteros, 2006; EUNIS, 2019; Montefalcone *et al*., 2021), although colonies also develop in caves and offshore circalittoral and upper bathyal rocks with and without crustose coralline algae (CCA) (Montefalcone *et al*., 2021). Recently, the term coral forest has been used to describe the structure and functioning of the biocoenoses dominated by habitat-forming anthozoans, including those dominated by red coral (e.g., Rossi *et al.,* 2017).

Along the Italian coasts, the distribution and structure of shallow-water populations (10-40 m) are widely known, thanks to the last 30 years of scientific research (Cannas *et al*., 2019). Our knowledge about the deeper populations, however, remains very limited, and the lower limits of the red coral forests are still unclear, considering that the professional fishermen do not operate below 135 m depth (Cannas *et al*., 2019).

Corallium rubrum is listed as "Endangered" in the Mediterranean Red List by IUCN (Otero *et al*., 2017), and the management of its harvesting and other conservation actions are included in several national laws, international conventions (Annex III SPA/BD, Bern), proposals, and European instruments, such as the Habitats Directive (1992) (GFCM 2011; Cannas *et al*., 2019). The coastal populations are often preserved within the boundaries of Marine Protected Areas (MPAs), while the conservation of the offshore, deeper forests appears to be more problematic, being frequently located off the limits of territorial waters (12 NM) and therefore not subjected to national laws. Additionally, these deep populations are often found below the limits of SCUBA harvesting and, theoretically, are no more exploitable by trawling gears since the European ban in 1994 (Council Regulation No 1626/94), which recognised the dramatic impact of ingegno and similar gears on red coral and other coralligenous components (Cattaneo-Vietti *et al*., 2017).

Nowadays, thanks to the extensive use of underwater technologies, such as Remotely Operated Vehicles (ROVs), it became feasible to explore environments unreachable by SCUBA diving. In the last 15 years, vast programs of characterisation of the mesophotic and bathyal benthic populations took place around the Italian coasts and offshore sites, up to 775 m of depth (Cau *et al*., 2015; Angiolillo *et al*., 2016; Corriero *et al*., 2019, Moccia *et al*., 2019; Enrichetti *et al*., 2020; Bo *et al*., 2020a, b; Consoli *et al*., 2021).

This paper provides a comprehensive assessment of red coral occurrence (based on presence/absence data) and relative abundance along Italian and neighbouring international waters. Data also include information on habitats' features that support the distribution of red coral. Moreover, a comparison of the recorded data with those of the historic fishing grounds (Cattaneo-Vietti *et al*., 2016) allowed to obtain information on the present status of the exploited populations.

Table 1. Technical information of the surveys conducted in the investigated areas.

Area	Survey	Year	ROV	Av. duration videos (h: min)
Liguria	Min. Ambiente - Corallo rosso*	2012	Pollux	0:50
	ARPAL-MS	2015-2016	Pollux	0:54
	ARPAL-MS	2018	BluROV2	0:45
	ARPAL-MS	2018	Chinook	0:58
Tuscan Archipelago	Min. Ambiente - Corallo*	2010, 2012	Pollux	0:53
	Concordia	2012	Pollux	1:03
Pontine Archipelago	ENPI - Ecosafimed	2014	Pollux	1:09
Gulf of Naples	Min. Ambiente – Corallo*	2010, 2012	Pollux	0:55
Sardinia E	Sardegna - Corallo rosso*	2011, 2013	Pollux	1:18
Sardinia W	Sardegna - Corallo rosso*	2011, 2013	Pollux	1:08
Sardinia NW	RAS - Regione Sardegna*	2012-2015	Prometeo, Flat Platform 6+	-
Calabria Tyrrhenian	MoBioMarCal	2007, 2008, 2009	Pollux	0:40
Calabria Ionian	MoBioMarCal	2008, 2009	Pollux	0:40
Apulia	CR - Deep coralligenous*	2010-2012	Mini Strait I	0:30
	POR Puglia 6.5a*	2014-2020	Mini Strait I	0:30
Aeolian Archipelago	Vulcani Eolie	2010, 2011, 2013, 2014	Pollux	1:35
	Milazzo	2014	Pollux	1:16
	ENPI - Ecosafimed	2014	Pollux	1:02
Egadi Archipelago	Min. Ambiente – Corallo*	2011	Pollux	1:03
Sicily Channel	Relitti	2010, 2012	Pollux	0:48
	Banchi	2012	Pollux	1:13
	Greenpeace	2012	Pollux	0:54
	Canale Sicilia	2011	Pollux	0:52
Seamounts	TyrSec	2009	Pluto	1:20
	ISPRA	2010, 2011, 2012, 2013	Pollux	1:00
	BioMount	2017, 2018	MultiPluto	1:00

* Surveys including sites indicated by red coral fishermen or known from historical archives for this species.

Material and Methods

In this study we considered two sets of data obtained from the analysis of ROV videos, where each video (or dive) corresponded to a distinct geographical site.

Dataset 1 included 503 ROV videos, made between 2007 and 2020, ranging from 40 m to 775 m. These surveys targeted the exploration of mesophotic hardgrounds with numerous campaigns, including sites indicated by red coral fishermen or known from historical archives for this species (Table 1). This dataset covered 12 main macro-areas: Ligurian Sea, Tuscan Archipelago, Pontine Archipelago, eastern and western Sardinia, Gulf of Naples and adjacent regions, Tyrrhenian Calabria, Ionian Calabria, Egadi Archipelago, Aeolian Archipelago and surrounding coastline, Sicily Channel, and Apulian coast (Fig. 1, Table 2). Additional 43 sites were considered, located on the summit areas of nine seamounts found in the Ligurian Sea, central Tyrrhenian Sea and South Tyrrhenian Sea, between 30 and 70 nautical miles (NM) from the nearest coast and explored from 60 m to 590 m (Table 2). Finally, eleven iron wrecks (2 in Liguria, 3 in Sardinia, 1 in Calabria, 5 in the Sicily Channel), located from 0.3 to 4 NM from the coast, were explored between 45 m and 170 m (Table 2). In total, approximately 560,000 m^2 of outcrops were investigated for more than 520 hours of ROV observations.

Dataset 2 included 322 ROV videos obtained in the framework of a campaign financed by the Autonomous Region of Sardinia targeting mesophotic hardgrounds to search for new red coral sites. All ROV dives were conducted from 2012 to 2015 off Alghero and Bosa (North-western Sardinia) along about 60 km of the coast (Carugati *et al*., 2020) (Fig. 1, Tables 1-2). This survey was used only to map the coral occurrence in this specific Sardinian sector.

Technical information related to the ROV surveys is given in Table 1.

Video footage was analysed using Apple Final Cut Pro X software (version 10.4).

The following information was obtained from each video. Substrate type was defined according to two categories: (1) outcropping rocks and (2) rocks covered by CCA. The slope was determined by the inclination of

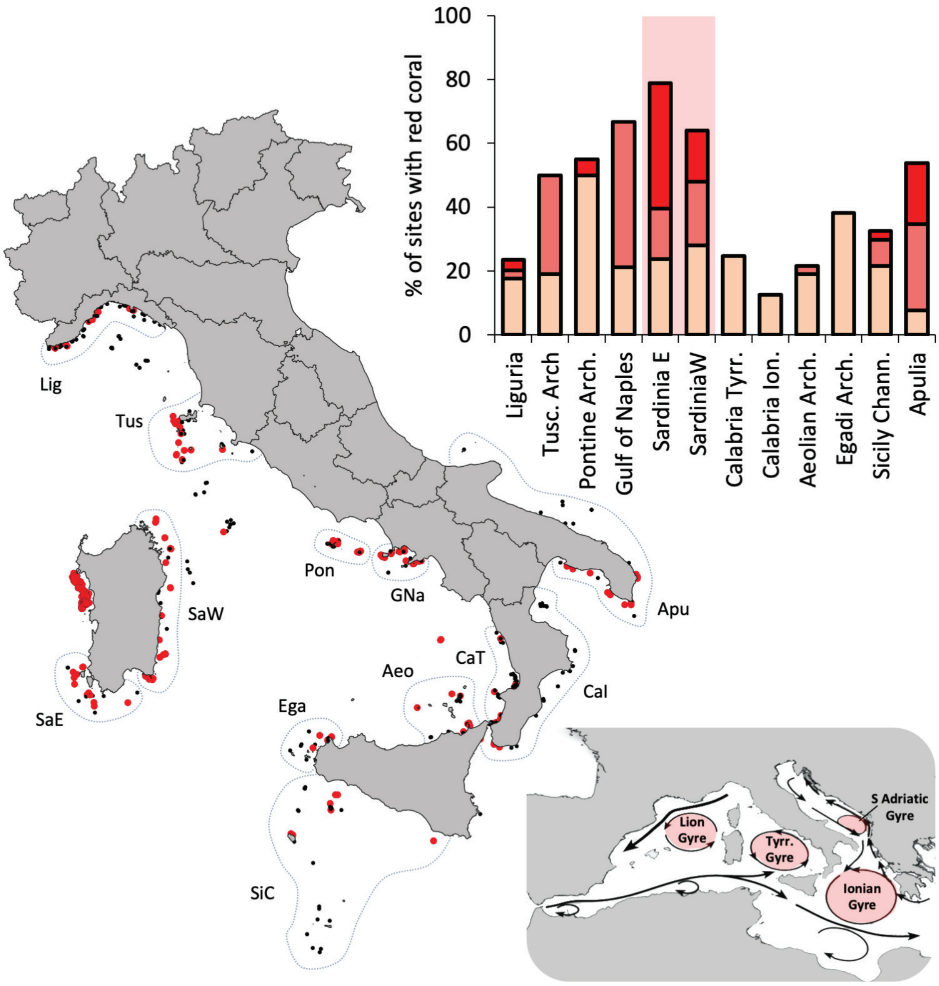

Fig. 1: Geographic distribution of the investigated sites showing the presence (red dots) or absence (black dots) of red coral. The histograms (upper inset) represent the percentage of sites with red coral in each considered macro-area (identified in the map by the dashed lines). The colours of the stacked bars indicate the percentage number of sites with scattered (light pink), aggregated (dark pink), and dense (red) populations. The pink box indicates the macro-areas encompassed in the red coral hotspot. The figure in the lower inset shows the shallow-water Mediterranean circulation with the gyres putatively involved in the evidenced red coral distribution.

Table 2. Presence of red coral along the Italian coasts and offshore seamounts according to the geographic macro-area, total number of sites (N°), number of sites with red coral (in brackets), average depths of the sites and of the sites with red coral, percentage composition of red coral populations according to the relative abundance.

Area	N°	Average depth all sites (m) ± SE	Average depth sites with red coral (m) ± SE	Population abundance (%) scattered (1)	aggregate (2)	dense (3)
Liguria	119 (28)	106.3 ± 10.8	95.2 ± 8.2	75.0	10.7	14.3
Tuscan Archipelago	42 (21)	81.7 ± 12.6	91.0 ± 5.6	38.1	61.9	0.0
Pontine Archipelago	20 (11)	118.4 ± 14.4	102.7 ± 9.5	90.9	0.0	9.1
Gulf of Naples	33 (22)	105.9 ± 6.5	95.2 ± 4.6	31.8	68.2	0.0
Sardinia NW	322 (306)	115.3 ± 0.5	107.7 ± 0.2	61.4	32.4	6.2
Sardinia E	38 (30)	147.7 ± 11.3	130.8 ± 5.4	30.0	20.0	50.0
Sardinia W	25 (16)	146.0 ± 15.3	113.1 ± 6.6	43.8	31.2	25.0
Tyrrhenian Calabria	73 (18)	100.9 ± 3.9	99.0 ± 5.9	100.0	0.0	0.0
Ionian Calabria	32 (4)	84.5 ± 7.5	72.5 ± 8.3	100.0	0.0	0.0
Aeolian Archipelago	37 (8)	102.6 ± 7.2	95.0 ± 10.2	87.5	12.5	0.0
Egadi Archipelago	21 (8)	118.4 ± 11.6	103.4 ± 5.3	100.0	0.0	0.0
Sicily Channel	37 (12)	108.0 ± 10.6	127.7 ± 9.7	66.7	25.0	8.3
Apulia	26 (14)	108.1 ± 29.4	62.8 ± 2.8	14.3	50.0	35.7
Seamounts						
Ulisse	5	437.5 ± 20.7				
Penelope	3	470.0 ± 10.1				
Occhiali	4	401.9 ± 50.3				
St. Lucia	6	185.1 ± 10.4				
Cialdi	4	465.0 ± 59.1				
Etruschi	4	371.9 ± 4.3				
Baronie	4	343.5 ± 50.0				
Vercelli	8 (1)	281.9 ± 51.0	(111)			
Palinuro	5 (2)	148.4 ± 16.5	(121, 195)			
Iron Wrecks						
Liguria	2	70, 102				
Sardinia E	3	45, 95, 170				
Calabria Tyrr.	1	130				
Sicily Channel	5	45, 50, 65, 72, 160				

the hardground hosting red coral using three categories: horizontal (< 20°), sloping (20°-60°) and (sub)vertical (> 60°). The dominance of a substrate type or an inclination level was defined if it persisted in the observations of the hardgrounds for more than 75% of the video time. For each video, the relative abundance of the colonies was reported in terms of (1) scattered colonies (< 2 colonies m^{-2}), (2) aggregated colonies (2-10 colonies m^{-2}) or (3) dense colonies (> 10 colonies m^{-2}).

The number of sites with presence of red coral was calculated for each considered macro-area, and data were reported as percentage occurrence according to the relative abundance of the species.

The normalised number of sites with red coral was obtained for each macro-area (excluding NW Sardinia) at eight depth ranges (< 50 m, 50-75 m, 75-100 m, 100-125 m, 125-150 m, 150-175 m, 175-200 m and > 200 m). The resulting bathymetric distribution of the species was presented as a correlation between depth and percentage of sites with red coral expressed as average (± SE) of all the macro-areas per each considered range (with n, n° of macro-areas, varying between 6 and 12). In addition, the depths of the dives and the depths at which red coral was recorded in each site were used to build comparative Box-Plot distributions for each macro-area.

The average percentage of sites with red coral presence was calculated also according to substrate type (rocks, R, and rocks encrusted by CCA, C) and slope (horizontal, H; sloping, S; vertical, V) in three depth ranges (<100 m, 100-150 m, and >150 m) depicting the percentage contribution of each category of relative abundance. Means were calculated considering the macro-areas in each depth range (n varying between 7 and 12 for substrate and between 3 and 12 for slope). SE was calculated on the average total percentage, independently from the relative abundance of the populations. The bathymetric trends of occurrence of substrate type (rocks and CCA-covered rocks) on the whole dataset, independently from the red coral presence, were also calculated.

Differences in red coral average occurrence were tested for two factors: "Substrate" (fixed, 2 levels, nested within "Depth") and "Slope" (fixed, 3 levels, nested within "Depth") using PERMANOVA analysis; additionally, pairwise comparisons were made to assess which levels were significantly involved (Anderson *et al*., 2001). The statistical analysis was performed with PRIMER7 software (Primer-e, Auckland, New Zealand).

Cattaneo-Vietti *et al*. (2016) reported a detailed overview of the harvesting effort in all Italian areas considered here and created a map of the commercially exploited banks' distribution along the Italian coasts in the last two centuries, thanks to historical and recent papers (Gaetani, 1867; Panceri, 1871; Targioni-Tozzetti, 1880; Canestrini & Canestrini, 1883; Parona, 1883; Colombo, 1887; Lo Bianco, 1909; Mazzarelli, 1915, 1931; Mazzarelli & Mazzarelli, 1918; Peruzy, 1923; Scatizzi, 1935; Marini & Ferru, 1989; Errico & Montanelli, 2008; Cattaneo-Vietti & Bavestrello, 2010; Gangemi, 2011, 2014; Santangelo *et al*., 2007, 2012; Mercurio *et al.*, 2012; Priori *et al*., 2013; Bramanti *et al*., 2014). This map was transferred to a QGIS platform as raster data. The georeferencing tool was applied to this digitalised, non-metrical map in the geo-workspace to point off the non-metrical map with known or given coordinates, called ground control points, using the TPS (Thin Plate Spline) transformation algorithm (Favretto, 2012). Hence, it was possible to conduct concordance analyses between historical and recent point layers using this map as a reference (Barsanti *et al*., 2007). Around old points, a buffer zone of 500 m, a measure equal to the maximum residual value reported by the ground control points, was created to verify other latent concordances, assuming possible errors in the georeferencing process or the lack of precise location of historic data. The final map used the intersection tool to identify points that were shared between the two layers: when a recent point fell into the buffer zone of an ancient point, the two points were considered concordant; otherwise, they were considered discordant. The number of revisited sites reporting the current relative abundance of red coral was also calculated for eight macro-areas.

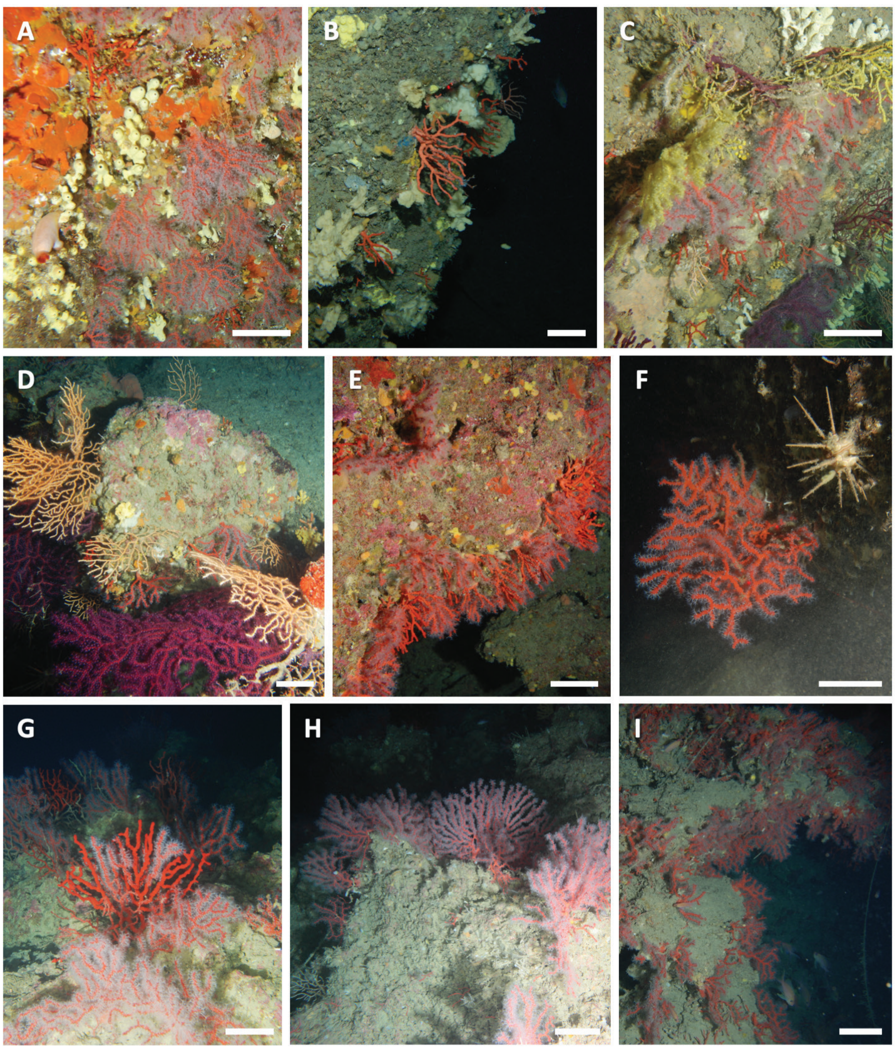

Fig. 2: Examples of benthic communities, including red coral, found during the surveys. A) A rich sponge (mainly *Aplysina cavernicola*) and *Corallium rubrum* assemblage at about 65 m on a vertical cliff (Montecristo Island, Tuscan Archipelago). B) Sparse sponges and red coral colonies at 105 m depth on a vertical substrate along the Tyrrhenian Calabrian coast. C) *C. rubrum* and the gorgonian *Paramuricea clavata* on a sub-vertical cliff at 85 m depth (Ischia Island, Gulf of Naples). D-E) The typical red coral facies on coralligenous outcrops at 65 m (Gulf of Salerno) and at 85 m (Punta delle Oche, SW Sardinia). F) A solitary colony on Palinuro Seamount (121 m). G-I) Red coral colonies growing upwards on carbonatic platforms in the Sicily Channel, respectively off Ragusa (85 m) (G) and Graham Bank (120 m) (H), and at 115 m on San Pietro Island (SW Sardinia) (I). Scale bar: 10 cm.

Results

The analysis of the video footage revealed that red coral populations were present in 35% of the explored sites included in dataset 1 (ranging from 12.5% in Ionian Calabria to 78.9% in E Sardinia) and in 95% of the sites in NW Sardinia (dataset 2) (Fig. 1).

Corallium rubrum was recorded as a component of very different communities according to depth and substrate type. At lower depths, on CCA-covered substrata, red coral was often found in mixed assemblages coupled with sponges, particularly *Aplysina cavernicola* (Vacelet, 1959) (Fig. 2A, B) and gorgonians, mainly *Paramuricea clavata* (Risso, 1826) and *Eunicella cavolini* (Koch, 1887) (Fig. 2C, D). Red coral created dense monospecific assemblages on vertical cliffs and overhangs, especially on the outer rim of rocky terraces (Fig. 2E). Often, large red coral colonies represented the only megabenthic organisms over horizontal bottoms on deep offshore outcrops (Fig. 2F-I).

In several cases, red coral populations were prone to strong mechanical injuries due to a large number of derelict fishing gears lost on rocky bottoms (Fig. 3A-D). Except for one Sicilian site (Cattaneo *et al.*, 2017), no evident traces of ingegno (e.g., accumulation of red coral debris, pieces of nets) were found. In some cases, particularly along the SE Sardinian coasts, dramatic mesophotic mass mortalities were recorded, with several colonies completely deprived of coenenchyme. Dead colonies were found intact, attached to their substrate, with the exposed calcareous scleraxis covered by a large amount of encrusting epibionts (Fig. 3E, F). Finally, during dives conducted in the Tuscany Archipelago at a depth of 80-90 m, the first evidence of putative predation was documented by the starfish *Peltaster placenta* (Müller & Troschel, 1842) on red coral colonies (Fig. 3G-I).

Geographic distribution and abundance patterns

The analysis of the video archive allowed us to clarify the distribution of mesophotic and upper bathyal red cor-

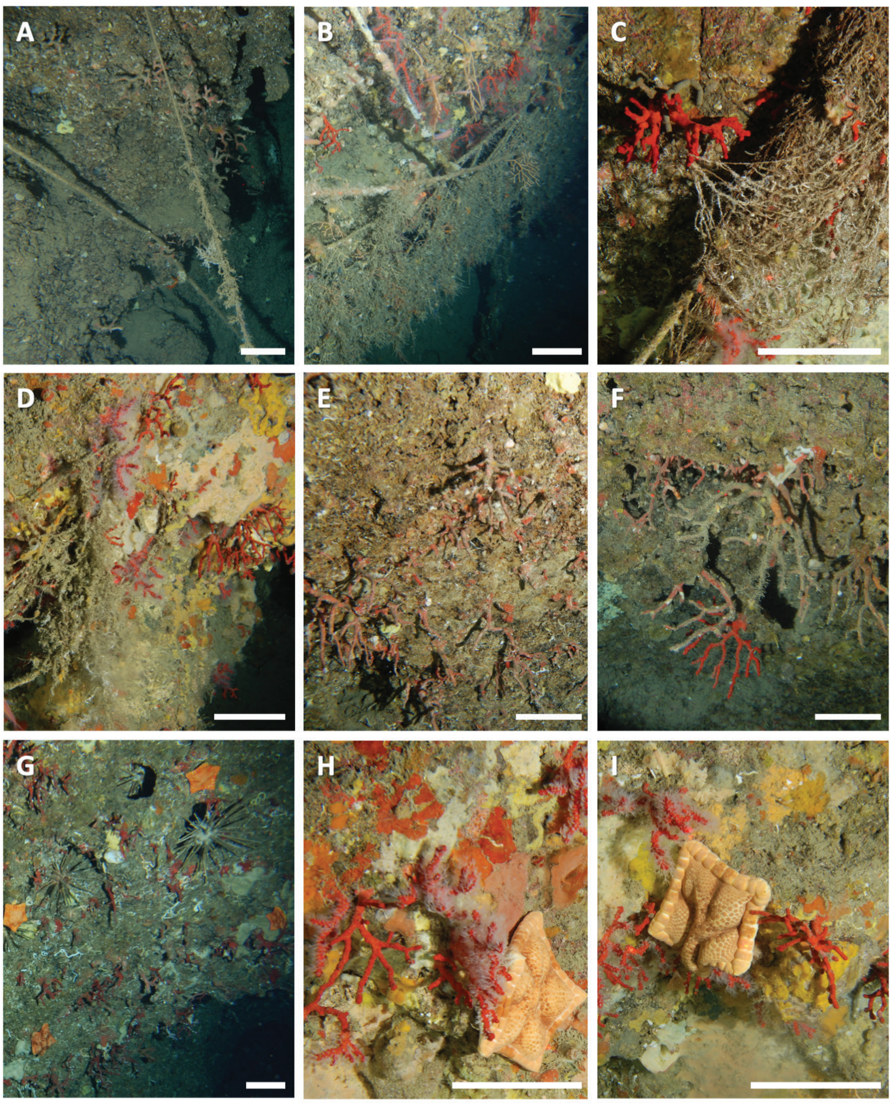

Fig. 3: Mechanical injuries to red coral populations due to derelict fishing gears (A-D). Evidence of mesophotic red coral mass mortalities at Carbonara Cape (SE Sardinia, 120 m) (E) and in the Salerno Gulf (S Tyrrhenian, 100 m) (F). First evidence of predation by the starfish *Peltaster placenta* on red coral colonies (G-I). Scale bar: 10 cm.

al forests within the considered macro-areas, highlighting different occurrences and relative abundances (Table 2; Fig. 1). At the basin scale, red coral populations were recorded in all the explored macro-areas. Nevertheless, the highest occurrences (> 50%) referred to a wide area, including the central Tyrrhenian Sea (Tuscan Archipelago, Pontine Archipelago, Gulf of Naples, and eastern Sardinia), the western Sardinian coast, and the Apulian coast (Fig. 1, upper inset). In the other explored areas, the occurrences were lower, ranging from 38% in the Egadi Archipelago to about 13% along the Calabrian coast of the Ionian Sea.

Deep populations were also searched over nine offshore seamounts. The species was recorded, with scattered colonies, only on the Vercelli Seamount at a depth of 111 m and on the Palinuro Seamount at 121 m and 195 m (Table 2). No colonies were found on the explored iron wrecks (Table 2). In three areas, high abundances of red coral were found in the proximity of wrecks, specifically at 1 km in Liguria (Portofino Cape), 4 km in SE Sardinia (Carbonara Cape), and 18 km in Calabria (St. Eufemia Gulf).

Although only semi-quantitative abundances were estimated, areas showing high densities (> 10 colonies m^{-2}) were primarily present in E and W Sardinia and Apulia. In the other considered areas, red coral occurred mainly with aggregated (2-10 colonies m^{-2}) or scattered (< 2 colonies m^{-2}) populations (Table 2; Fig. 1, upper inset).

Depth distribution and habitat preference

The red coral populations were found between 40 m and 247 m, but the highest occurrences were recorded between 75 m and 175 m (Fig. 4). Populations composed of aggregated and dense colonies represented more than 50% of the total down to 100 m, and this percentage progressively decreased according to depth. From 150 m, populations were composed only of scattered colonies. Red coral occurrence was significantly correlated with depth (R = 0.9357). From a geographic perspective, it is possible to recognise a mesophotic red coral belt (75-125 m) along the whole Italian coast. The belt was shallower in Ionian Calabria and Apulia, while it became deeper in E Sardinia and Sicily Channel (Fig. 5).

Hard substrata recorded during the analysed dives were divided into two classes based on the presence/absence of CCA coverage. Down to approximately 125 m, rocks with CCA coverage represented the most commonly available hard substratum. Below this threshold, rocks without algal coverage progressively became more frequent, and below 250 m, no algal coverage was recorded (Fig. 6A). Red coral colonies were observed settled both on coralligenous concretions and rocky substrata but with a preference for biogenic habitats, as confirmed by the statistical analysis (p = 0.0166) (Table 3), especially in the < 100 m depth range (Fig. 6B; Table 4).

Moreover, a strong preference for sub-vertical substrata was recorded and statistically confirmed (p = 0.0003) (Table 3). There was a progressive increase in the percentage occurrence of red coral from horizontal to vertical sites, as shown by pairwise comparisons. The recorded pattern was mirrored at all examined depth ranges (Table 4; Fig. 7).

Past and present of exploited banks

In the present work, 118 ROV sites fell inside the buffer zone of 500 m created around the historical coral banks exploited for some periods in the past two centuries. Red coral was recorded in 102 of these sites, while colonies were no longer observed in the remaining ones. All the revisited sites in E and W Sardinia and Apulia still hosted

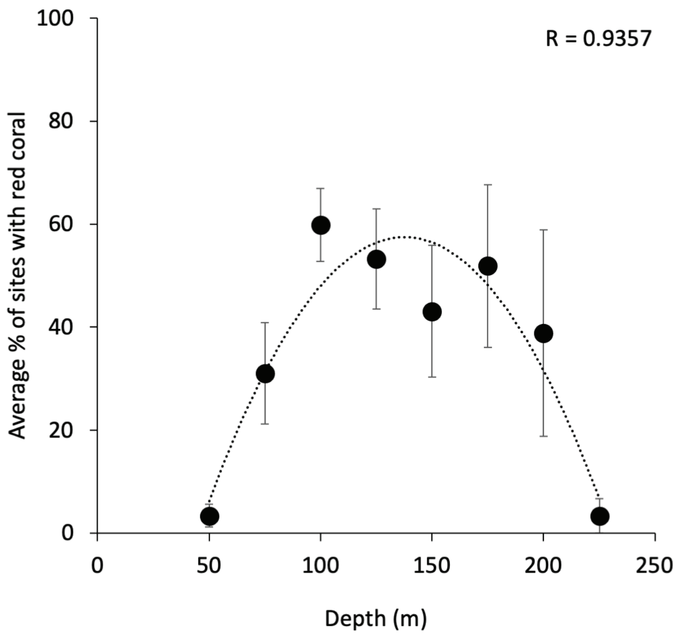

Fig. 4: Correlation between depth and percentage of sites with red coral expressed as average (± SE) of all the macro-areas per each considered range.

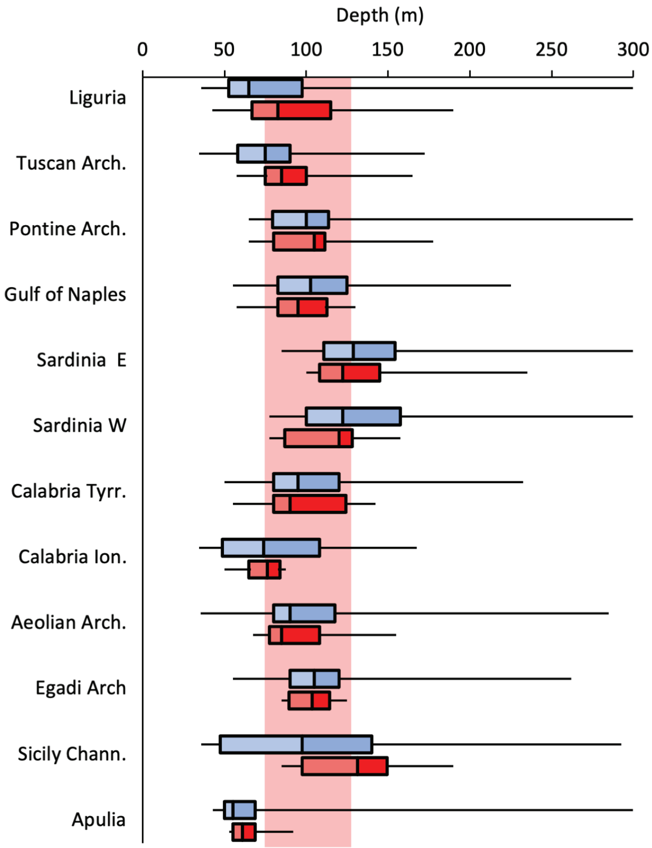

Fig. 5: Bathymetry. Box plots depicting the depth distribution of all the sites (blue boxes) and of the sites with red coral (red boxes) in each considered macro-area. The pink box indicates the mesophotic red coral belt.

red coral populations (Fig. 8 and inset). In contrast, in Sicily and Calabria, from 40% to 50%, respectively, of the historical sites did not have red coral colonies. In all the other areas, the number of old sites currently without coral was between 6 and 10%. The highest relative abundances were mainly recorded in E Sardinia (Fig. 8, inset).

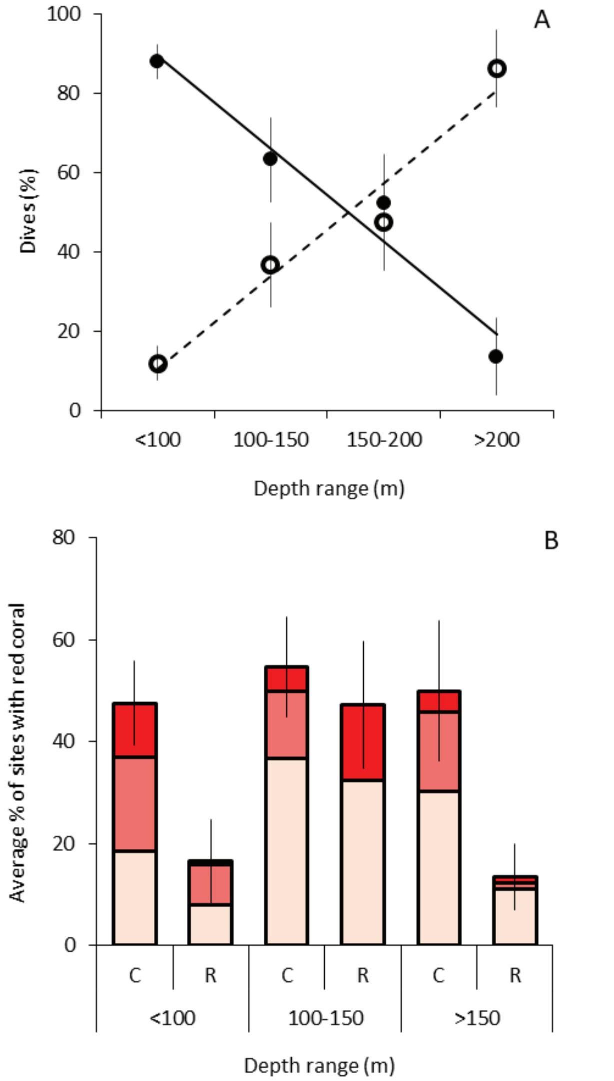

Fig. 6: Substrate type. A) Average percentage of sites (± SE) dominated by rocky outcrops (empty dots, dashed line) and by CCA-covered hard substrates (full dots, solid line) with depth. B) Average percentage of sites with red coral (means of macro-areas ± SE) according to substrate type (C, CCA-covered hard substrates, R, rocky outcrops) in three depth ranges. The colours of the stacked bars indicate the percentage number of sites with scattered (light pink), aggregated (dark pink), and dense (red) populations.

Table 3. PERMutational Analysis of variance (PERMANOVA) performed on the percentage occurrence of red coral, calculated for the two factors "Substrate" (fixed, 2 levels, nested within "Depth") and "Slope" (fixed, 3 levels, nested within "Depth"). Significant results are shown in bold.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Depth	2	7415.7	3707.9	14.467	0.1176	9903
Substrate (Depth)	3	14678	4892.7	1.909	**0.0166**	9892
Res	51	1.31E+09	2563			
Total	56	1.54E+09				
Depth	2	6432.1	3216.1	13.605	0.153	9900
Slope (Depth)	6	32806	5467.6	2.313	**0.0003**	9875
Res	68	1.61E+09	2363.8			
Total	76	2.02E+09				

Table 4. Pairwise tests. Significant results are shown in bold.

PAIR-WISE TESTS			**Unique**
SUBSTRATE	**t**	**P(perm)**	**perms**
Within level '<100' of factor 'Depth'	19.005	**0.0083**	5869
Within level '100-150' of factor 'Depth'	0.76495	0.7835	7448
Within level '>150' of factor 'Depth'	1.287	0.0822	266
SLOPING			
Within level '<100' of factor 'Depth'			
H vs S	19.993	**0.0026**	6998
H vs V	2.475	**0.0001**	2048
S vs V	31.445	**0.004**	3725
Within level '100-150' of factor 'Depth'			
H vs S	0.85286	0.595	5046
H vs V	10.463	0.2816	244
S vs V	0.76342	0.7787	516
Within level '> 150' of factor 'Depth'			
H vs S	14.018	**0.0545**	184
H vs V	10.158	0.2889	19
S vs V	10.759	0.2191	60

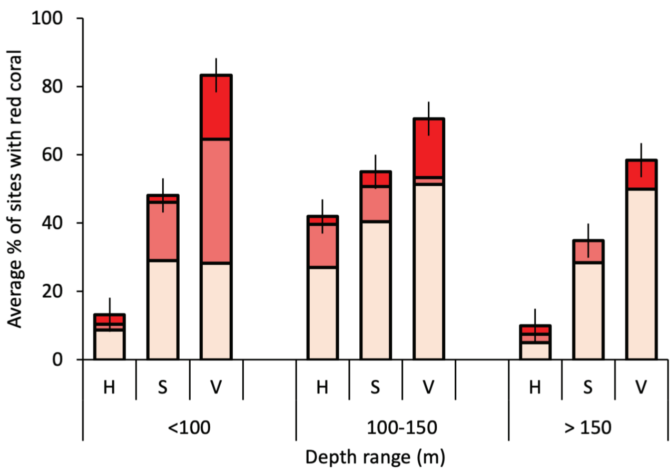

Fig. 7: Substrate inclination. Average percentage of sites with red coral (means of macro-areas ± SE) on substrates with different inclinations (H, horizontal; S, sloping; V, vertical) in three depth ranges. The colours of the stacked bars indicate the percentage number of sites with scattered (light pink), aggregated (dark pink), and dense (red) populations.

Discussion

The analysis of the largest available dataset regarding *Corallium rubrum* along the Italian coasts allows us to evaluate the occurrence (based on presence/absence data), relative abundance, and habitat characteristics of the mesophotic and upper bathyal red coral populations at a basin scale.

From the geographical point of view, the results highlight the presence of this species in all the explored areas, although with relevant differences. The highest occurrences were recorded in Sardinia. The peak registered along the NW Sardinian coast over a relatively limited stretch of coast was derived from a monitoring design less randomised than the main dataset; nevertheless, the high occurrence was plausible and historically documented (Carugati *et al*., 2020). In the central Tyrrhenian Sea, red coral mainly occurred in the Tuscany and Pontine archipelagos and the Gulf of Naples and surrounding areas. Occurrences were lower to the northern and southern of this Tyrrhenian red coral hotspot, as in the Ligurian, Calabrian, and Sicilian coasts. Present data about the occurrence of red coral banks along the Ligurian coast confirmed the fragmented distribution of this species in this area (Cattaneo-Vietti *et al*., 2016). A similar situation was observed along the Tyrrhenian Calabrian coasts and around Sicily. With regard to the Italian Adriatic coasts, the occurrence of red coral was limited to the Apulian coasts.

Even though the factors potentially explaining this large-scale distribution pattern are difficult to disentangle and may include local differences in the physical-chem-

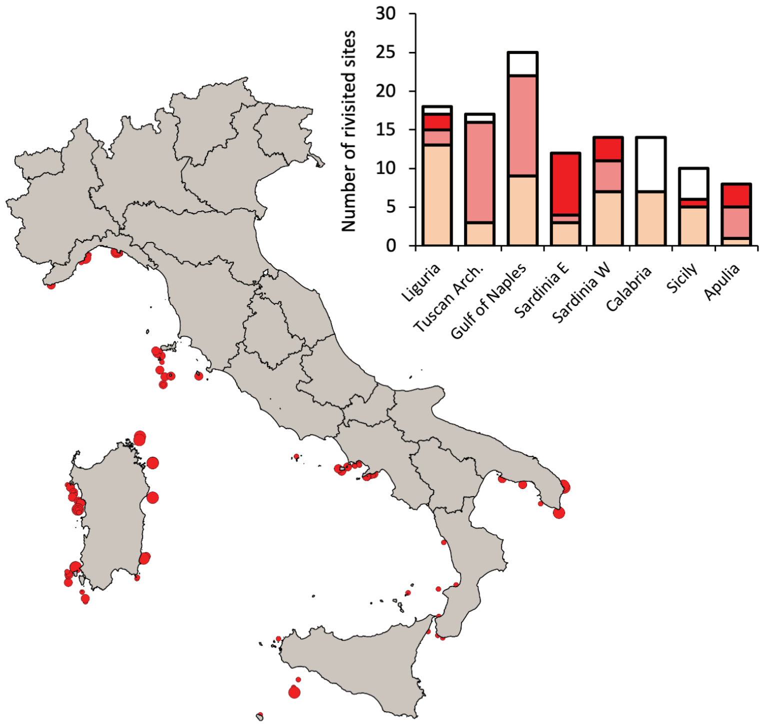

Fig. 8: Distribution map of the revisited historical fishing grounds (Cattaneo-Vietti *et al*., 2016) in which red coral colonies were still observed. The histograms show the number of sites revisited per macro-area. Colours of the stacked bars indicate the number of sites with scattered (light pink), aggregated (dark pink), and dense (red) populations. White bars represent the fishing grounds today recorded without coral colonies.

ical characteristics of the water, settling patterns, biogeographic discontinuities, trophic inputs, silting levels, and competition, it is worth mentioning the circulation pattern of the surface water (0-300 m) (Fig. 1, bottom inset). Four mesoscale gyres (Lion Gyre, Tyrrhenian Gyre, South Adriatic Gyre, and Ionian Gyre) (Vergnaud-Grazzini *et al*., 1988; Millot, 2005; Boero *et al.,* 2019) are present in the areas hosting the highest occurrences of red coral, suggesting an influence of the water mass circulation and trophic input on the observed distribution. The cold and rich Lion Gyre in the Balearic Sea could connect the western Sardinian populations with the Catalan ones (Linares *et al*., 2003) and may be responsible for the high red coral productivity in this area. Similarly, the Tyrrhenian Gyre could sustain red coral populations in the Tuscan Archipelago, E Sardinia, Egadi Archipelago, Aeolian Archipelago, Tyrrhenian Calabria, Gulf of Naples, and Pontine Archipelago. Finally, the South Adriatic Gyre connects eastern Apulian populations with Albanian ones (Tsounis *et al*., 2009), and the Ionian Gyre spreads the populations along the Apulian coasts. The involvement of gyre circulation in red coral dispersal agrees with the high pelagic larval duration and motility behaviour recently highlighted in laboratory experiments (Martinéz-Quintana *et al*., 2015). The Sardinian mesophotic red coral colonies are also characterised by high genetic diversity (Costantini *et al*., 2007b; Ledoux *et al*., 2010; Cannas *et al.*, 2016), which may support the maintenance of the hotspot. Indeed, it has been suggested that hydrological conditions enhance the mixing of the genetic pools in the Balearic region, while the persistence of the populations has been linked with the existence of putative glacial refugia for the species (Ledoux *et al*., 2010).

The virtual absence of red coral populations on the studied seamounts at depths and in environments suitable for the development of this species could be partially relatable to the difficulty of larvae in reaching offshore locations (Costantini *et al*., 2007a, 2011, 2013, 2016). However, other mesophotic habitat-forming anthozoans with putatively similar life traits thrive on these seamounts (Bo *et al*., 2011), and *C. rubrum* has been found in other Mediterranean offshore sites (Seco de Los Olivos Seamount) (De la Torriente *et al*., 2018), suggesting that different causes could be related, particularly productivity levels.

Within the general distribution pattern, a distinctive regional situation was observed in the Ionian Sea, where red coral was scarce on the Calabrian coast and widely present on the Apulian side (Fig. 1). The species was found in the Strait of Messina until the extreme tip of Calabria but seemed to be unable to overstep the close Spartivento Cape. On the other side of the Ionian Sea, the species crossed the Santa Maria di Leuca Cape and was abundantly found until Taranto. The distribution discontinuity along the western side of the Ionian Sea could be determined by hydrological boundaries limiting population connectivity (Villamor *et al*., 2014). Along the Calabrian side, larval dispersion is influenced by the main current direction of the Ionian Gyre flowing from East to West. Along the Apulian side, larvae are probably unable to cross a large area, from Taranto to Colonne Cape, where hard bottoms are scarce. The existence of phylogeographic boundaries in the central Mediterranean Sea was already suggested, on a genetic basis, to limit the connectivity of other benthic invertebrates (Villamor *et al*., 2014). In this regard, the spatial-genetic structuring analyses of mesophotic red coral populations generally indicate that strong barriers to gene flow occur among areas as well as among depth ranges (Costantini *et al*., 2011, 2013; Cannas *et al.*, 2015, 2016; Costantini & Abbiati, 2016). The red coral coldspot of the western Ionian Sea, however, does not entirely agree with historical information stating that in the mid-19th century, good amounts of red coral (1.7 tons) were fished from Spartivento Cape to Colonne Cape (Balzano, 1859; Gaetani, 1867). Moreover, red coral was recently observed by ROV at the Amendolara Bank at mesophotic depths (Canese, pers. comm.).

From a bathymetric perspective, a well-defined red coral belt was recognised in all the studied sites, indicating *C. rubrum* as a typical mesophotic-upper-bathyal species. No red coral colonies were recorded below 247 m, although hard substrata were still widely present. This evidence suggests that records at greater depths (Taviani *et al*., 2010; Knittweis *et al*., 2016) must be considered exceptional and probably related to peculiar local conditions allowing larval downwelling, settling and recruitment. The banks present below 135 m, being unreachable by professional fishermen (Cannas *et al*., 2019) and protected from illegal harvesting, are to be considered valuable pristine deep population sites when they are not impacted by other fishing activities.

Both geographical and bathymetric distributions could be partially related also to biomineralogical features. Although red coral is found both on coralligenous accretions and primary rocks, it shows a preference for biogenic habitats. It is known that the presence of a coralline algal layer can positively or negatively drive the settling of many benthic species in both tropical and temperate environments (Harrington *et al*., 2004; Ritson-Williams *et al*., 2009, 2014; Canessa *et al*., 2020). To date, experimental tests have shown that red coral larval settling did not show significant differences between *Lithophyllum stictaeforme* and bare rocks (Zelli *et al*., 2020); however, this approach should be applied to different crustose algae. None of the explored iron wrecks, mainly identified as modern boats not older than 60 years, hosted red coral colonies. The absence of colonies on wrecks in areas characterised by a high occurrence of red coral (e.g., SE Sardinia, Liguria, Calabria) suggests that this material could be unsuitable for the species' settling. The type of metal of a wreck, in fact, is known to influence the community composition of the fouling organisms (Peirano, 2013). The lack of literature records of red coral on iron could support this observation; however, the influences of water circulation, larval dispersal ability, as well as depth, status and biocoverage of the wreck needs to be verified with further targeted investigations.

The present observations also underline a significant influence of the substrate inclination in the settling of red coral colonies. In all the examined macro-areas, the percentage occurrence of coral colonies was directly related to the slope: the occurrence of colonies on (sub)-vertical walls (> 60°) was two to four times higher than on horizontal bottoms at any depth and on any substratum type. This result expands the traditional idea that deep red coral is mainly found on rocky boulders and plateaus (Rossi *et al*., 2008). Substrate inclination has been variously considered also by other authors. Cau *et al*. (2016) stated that mesophotic Sardinian populations composed of small and dense colonies dominated rocky vertical walls. In contrast, populations characterised by large and sparsely distributed colonies were found only on horizontal beds not covered by sediment. Considering the colony orientation and not the substrate inclination, Rossi *et al*. (2008) showed, through ROV footages, a variability according to depth. In shallow waters, colonies were present in small crevices, mainly with a downwards orientation. Down to a depth of 60 m, colonies were oriented facing upwards on horizontal bottoms or perpendicular to sub-vertical walls. Overall, sloping substrate emerged as one of the most relevant constraints in determining the red coral population structure, together with maturity stage, currents, trophic input, siltation, borers, and anthropogenic impact (Tsounis *et al*., 2006; Bavestrello *et al*., 2014).

The comparison between historical and recent data suggests that red coral populations in the study macro-areas have suffered local extinctions due to the harvesting pressure (14% of the revisited banks), as previously suggested by Bruckner (2009). According to IUCN criterion A (population size reduction), in two areas (Sicily and Calabria), the species qualifies as vulnerable and endangered, respectively. At a basin scale (including numerous known harvesting sites), red coral is still widely distributed, which could be due to its high genetic diversity (Cannas *et al.*, 2016) and early sexual maturity, which is reached in colonies 4-5 cm high and a few millimetres in diameter (Santangelo *et al*., 2003, 2004; Gallmetzer *et al*., 2010). Remarkably, the Sardinian red coral hotspot hosted the highest occurrence of the species even though the area was prone to a high harvesting effort for centuries (Parona, 1883; Cannas *et al*., 2010; Follesa *et al*., 2013; Carugati *et al.,* 2020; Cattaneo-Vietti *et al*., 2016; Cannas *et al*., 2019).

Beside occurrence, a quantitative analysis of the studied forests providing data on density and morphometry of the single populations will provide further insights into the current status and recovery capacity of these populations.

Large-scale ground-truth distribution data are very important for management and conservation purposes at a regional scale since they allow for a more comprehensive understanding of the extent of a certain species in an area and at different bathymetric ranges and represent valuable information that can be used to build and validate predictive habitat models. In addition, coupled to quantitative data, these distributions are essential for evaluating the structure of the populations and making interpretations of the connectivity patterns, allowing long-term monitoring programs to be carried out. With this type of dataset, it is necessary to implement a regional adaptive management plan for red coral, as recently established by the General Fisheries Commission for the Mediterranean (GFCM, 2017), in order to improve decision-making processes regarding the conservation of this resource.

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This paper is dedicated to the memory of Prof. Riccardo Cattaneo-Vietti, a world-renowned marine biologist and pioneer in the study of the ecology and biology of red coral.

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