Structure and status of the Italian red coral forests: What can a large-scale study tell?

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The precious coral *Corallium rubrum* (Linnaeus, 1758) is a charismatic
Mediterranean species. A recent large-scale investigation along the Italian
coast highlighted its widespread occurrence at mesophotic and upper
bathyal depths, especially on coralligenous and bathyal vertical hardgrounds.
The lack of morphometric data limited the considerations on the structure and
health status of the populations, fundamental to identify the most vulnerable
sites and the correct management actions. For this reason, a ROV dataset,
consisting of 624 dives carried out between 40 m and 1825 m in the Ligurian
Sea, Tyrrhenian Sea, and Sicily Channel, was analysed to extrapolate
quantitative data to describe the populations. Ten random frames were
obtained from each of the 170 sites hosting red coral. Density, height, and
entanglement were evaluated for about 15700 colonies counted in the frames.
The densest populations were mainly found between 40 m and 80 m, with a
clear latitudinal density decrease. The mesophotic populations were
characterized by both scattered and densely aggregated colonies, while the
bathyal ones were dominated by sparse colonies. This study identified 17 major
coral areas based on the geographic proximity of the sites hosting red coral and
their topographic and oceanographic affinity. The size-frequency distribution
of the heights was skewed towards the smaller classes in almost all populations,
with a modal class between 2 cm and 4 cm. This study depicted a stress
situation of the populations throughout the entire study area, which could be
correlated also to the long-term harvesting pressure carried out in the basins.
Two additional sources of direct mortality were pointed out in this study.
Entanglement to artisanal and recreational fishing gear interested about 18% of
the recorded colonies, mainly at mesophotic depths. Almost all populations
suffered from mechanical entanglement, with the highest percentages in the
Ligurian Sea and Sicilian areas. This study also highlighted a massive occurrence

of recent deep mortality events, mainly along the eastern and southern coast of Sardinia and in the Campanian Archipelago. Thirty sites with extensive patches of dead colonies still in place were reported from 70 m to around 200 m, but their formation remains unclear.

Introduction

The precious coral *Corallium rubrum* (Linnaeus, 1758) is a charismatic Mediterranean species that suffered extensive exploitation for centuries due to its commercial value in the jewellery industry (Tsounis et al., 2006; Bussoletti et al., 2010; Cattaneo-Vietti and Bavestrello, 2010; Tsounis et al., 2010; Cattaneo-Vietti et al., 2017; Cannas et al., 2019). Harvesting has been traditionally exercised with non-selective and highly destructive trawling gear, while, after their ban in 1994, it has been carried out selectively by professional SCUBA divers; this long-term pressure resulted in a serious over-fishing that put this resource into jeopardy (Cattaneo-Vietti et al., 2017). Currently, this species is included in a number of international conventions supporting its controlled harvesting (SPA/BD Protocol Annex III, Bern Convention Annex III, Habitat Directive Annex V and GFCM Recommendations), and in 2016 it was assessed as Endangered in the IUCN Anthozoans Red List for the Mediterranean Sea (IUCN, 2016), recognizing its important ecological role as habitat-former (Garrabou and Harmelin, 2002; Rossi et al., 2017) and its decline over time. Taking into consideration the IUCN assessment, the inclusion of red coral in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) should be re-evaluated in the near future (Bruckner, 2009; Bussoletti et al., 2010; Bruckner, 2014).

In the past decades, in order to evaluate the distribution and status of the different populations living in the Mediterranean Sea, numerous research studies have been conducted, mainly on littoral banks, often showing an evident state of suffering (FAO, 1988; Cicogna and Cattaneo-Vietti, 1993; Cicogna et al., 1999; Garrabou and Harmelin, 2002; Santangelo et al., 2007; Santangelo et al., 2009; Santangelo and Bramanti, 2010; Tsounis et al., 2010; Bramanti et al., 2014; Montero-Serra et al., 2015). Dramatic size and structural shifts in shallow-water populations have been recognized (Bruckner, 2009), with "forest-like" populations, dominated by large, branched colonies of 30-50 cm height (10-30 mm in diameter) turning into "grass plain-like" populations, dominated by small colonies of 3-5 cm height (5-7 mm in diameter) (Garrabou and Harmelin, 2002; Tsounis et al., 2006; Santangelo et al., 2007; Tsounis et al., 2007; Bramanti et al., 2014). The size shift due to harvesting is not only related to the obvious reason that divers tend to select colonies of larger size, but also to the freeing up of space due to heavy harvesting enhancing larval settling events (Cerrano et al., 1997). The "grass plain-like" condition may persist for a long span of time, because of intra-specific competition (Tsounis et al., 2006), and only in a few Marine Protected Areas has a reversion been recognized after a long-term protection (Bavestrello et al., 2015; Richaume et al., 2021). Moreover, besides harvesting, other factors are known to threaten red coral populations, both direct (e.g., fishing activities and mass mortalities putatively linked to episodic and highly energetic events, like heat waves and volcanic eruptions) and indirect (e.g., climate change-driven events) (e.g., Cerrano et al., 2013; Bavestrello et al., 2014; Lodolo et al., 2017; Cau et al., 2018; Galgani et al., 2018; Enrichetti et al., 2019a).

From a conservation point of view, morphometric data are essential to estimate the health status of the populations, which, in turn, are fundamental to identify the most vulnerable sites and the correct management actions. Although several pieces of evidence are available for shallow-water populations, very little data have been recorded about the morphometric structure of deep populations (Rossi et al., 2008; Priori et al., 2013; Angiolillo et al., 2016; Cau et al., 2016; Carugati et al., 2022). These studies, mainly conducted on a local or regional scale, showed that deep-dwelling populations are generally less harvested than the shallow-water ones, even if high percentages of the colonies are still above the commercial size (≥ 7 mm of basal diameter). However, authors do not agree if there is a size-density relationship in red coral populations with increasing depth, presenting contrasting results.

A recent large-scale investigation along the Italian coast (Toma et al., 2022), taking advantage of an extensive ROV archive, demonstrated that, at basin scale, red coral still shows a wide occurrence, particularly in a large region of the central

Tyrrhenian Sea including Tuscan Archipelago, Pontine Archipelago, Gulf of Naples, and the Sardinian coasts. This study also demonstrated that the species occurrence peaks in the mesophotic zone, between 75 m and 125 m, showing a marked preference for biogenic habitats dominated by Crustose Coralline Algae (CCA) and for vertical substrata. However, the lack of morphometric data limited the considerations on the structure and health status of the populations.

The objectives of this study, therefore, were to i) conduct a large-scale morphometric survey on mesophotic and deep populations in the Ligurian Sea, Tyrrhenian Sea, and Sicily Channel, and highlight latitudinal and bathymetrical patterns in colony average size and density, ii) identify the size-frequency patterns in the most representative forests to depict the putative influence of harvesting pressure, and, ultimately, iii) identify other sources of direct mortality which may affect the health status of those populations.

Materials and methods

A large ROV archive was analysed to extrapolate quantitative data with the aim of describing the red coral populations present along the Italian coast. The dataset consisted of 624 ROV dives (each corresponding to a distinct geographical site) carried out between 2006 and 2021 in the Ligurian Sea, Tyrrhenian Sea, and Sicily Channel, between 40 m and 1825 m. Sites were grouped in localities based on their geographic proximity (maximum distance about 5 km), then localities were grouped in areas based on their topographic and oceanographic affinity (e.g., promontory, gulf, shoal), and such areas fell into different macro-areas (4 coastal ones, LIG Ligurian Sea, NCT North-central Tyrrhenian Sea, ST South Tyrrhenian Sea, and SC Sicily Channel, and 1 offshore, SEAM Seamounts) (Table 1).

The number of sites in which *Corallium rubrum* was present was counted and reported as a percentage of occurrence in the whole dataset. For the quantitative analyses regarding coral areas, only sites (hence localities and areas) with more than 30 colonies were considered.

The depth ranges at which red coral was recorded were noted and ten random frames were obtained for each site targeting the densest coral patches, for a total of 1700 analysed frames. For each picture, density was calculated considering the hardground surface, evaluated using the ROV laser beams, and the exact number of colonies, counted using ImageJ (15730 total counted colonies). The resulting average density of the sites was then defined according to three categories: (1) scattered colonies (< 5 colonies m^{-2}), (2) densely aggregated colonies (5-20 colonies m^{-2}) or (3) very densely aggregated colonies (> 20 colonies m^{-2}). Density values attributed to each category were based on the entire available dataset.

The relationship between density and depth was presented with two different approaches. The first considered the average densities of the sites in four distinct depth ranges (40-80 m, 80-150 m, 150-200 m, and > 200 m). The second analysis considered the percentage distribution of the density categories in the same depth ranges. These latter corresponded to the deepest part of the continental shelf, the shelf break, the upper bathyal range of the continental slope and seamounts, and the bathyal, respectively. The putative effect of latitude on the population average density per macro-area was also investigated by means of a linear regression with r = Pearson's correlation coefficient.

The height of the colonies was measured in each frame with ImageJ using the laser beams as a reference, to evaluate the morphometry of the populations in the selected coral areas. The relationship between height and depth was investigated by considering the mean height of the populations in the four depth ranges. The putative effect of latitude on the average height was also investigated in the macro-areas by means of a linear regression with r = Pearson's correlation coefficient. Finally, size-frequency graphs were created for the considered geographic areas, with size classes of 2 cm.

Entanglement to lost fishing gear was evaluated by noting the number of impacted colonies in each frame. Data were presented as the percentage of entangled colonies on the total, as well as the percentage of entangled colonies in each coral area. To investigate the correlation between entanglement and depth, the percentage of entanglement for each area and depth ranges were considered. The putative effect of latitude on the percentage of entanglement of the populations was also investigated for the macro-areas by means of a linear regression with r = Pearson's correlation coefficient.

Finally, in the sites where dead in-place colonies deprived of living coenenchyme were observed, ten random frames were collected and data of density, height, entanglement, substrate type (rocks, R, and rocks encrusted by CCA, C), and slope of the hardground where *C. rubrum* was attached were noted to characterize the mortality patches. In the sites where both living and dead populations were present, density values and the average height of the colonies were compared to evaluate the entity and timing of the mass mortality events.

Significant differences in terms of average densities and average heights in the selected coral areas were tested through a Kruskal-Wallis test (data not normally distributed, square root transformed, n=10 - 220, and n=35 - 2913, respectively, for 17 coral areas). Significant differences between average densities, average heights, and average entanglement in the four considered depth ranges were tested through a Kruskal-Wallis test (data not normally distributed, square root transformed, n=3 - 170, for the four depth ranges). All statistical analyses were performed using PAST Software ver. 4.03 (Hammer et al., 2001).

TABLE 1 Presence of *Corallium rubrum* along the Italian coast according to macro-area, coral areas (code in brackets), locality, number of sites per locality, latitude, and longitude of the centroid of the locality, depth range, average density and height, and percentage of entanglement of red coral populations in the locality.

Macroarea	Coral area	Locality	n° Sites	Lat	Long	Depth range (m)	Av. Density ± SE	Av. Height ± SE	Ent. (%)
LIG	Sanremo (SAN)	Bordighera	3	43.7800	7.6821	60-100	9.7 ± 2.5	2.6 ± 0.1	29.5
		St. Stefano	1	43.8090	7.8928	85-90	13.1 ± 1.5	6.1 ± 0.2	52.2
		Bordighera Canyon	3	43.7637	7.6908	64-212	1.3 ± 0.5	5.3 ± 0.3	78.7
		Arma di Taggia Canyon*	1	43.7850	7.9184	90-100	2.4 ± 0.6	2.7 ± 0.2	30.4
	Savona (SAV)	Finale Ligure*	2	44.1441	8.3474	85-100	0.6 ± 0.3	3.5 ± 0.5	10.0
		Lua Canyon*	1	44.1617	8.4093	95-100	2.6 ± 0.9	1.7 ± 0.2	0.0
		Maledetti Shoal	8	44.2257	8.4597	55-105	12.8 ± 2.3	6.2 ± 0.1	33.9
		Mantice Shoal*	1	44.2706	8.5226	120	0.2 ± 0.1	4.0 ± 1.0	100.0
	Portofino Promontory (PP)	Isuela	2	44.3203	9.1445	40-50	53.8 ± 4.2	5.3 ± 0.1	28.0
		Cala Inglesi	1	44.3058	9.1907	40	6.1 ± 3.3	6.0 ± 0.3	0.0
		Punta del Faro	3	44.2926	9.2231	55-65	9.7 ± 1.5	6.2 ± 0.2	16.4
NCT	Tuscan Archipelago (TA)	Elba Is.	6	42.7264	9.9925	60-110	25.3 ± 2.7	5.4 ± 0.1	12.3
		Pianosa Is.	4	42.7931	9.9824	70-90	11.8 ± 1.6	4.1 ± 0.1	6.1
		Montecristo Is.	7	42.3078	10.1871	60-170	18.4 ± 2.4	6.3 ± 0.1	0.0
		Giglio Is.	2	42.3100	10.9183	94-105	20.1 ± 3	4.7 ± 0.1	55.2
	Pontine Archipelago (PA)	Palmarola Is.	3	40.9789	12.8438	73-120	3.4 ± 0.7	2.6 ± 0.1	0.0
		Ponza Is.	6	40.9570	12.9873	66-193	8.8 ± 2.2	3.9 ± 0.1	7.3
		Zannone Is.	2	40.9777	13.1189	90-120	4.8 ± 1.1	5.3 ± 0.3	58.2
	NE Sardinia (NES)	Caprera Canyon	3	41.3409	9.6349	111-144	10.9 ± 0.9	2.9 ± 0.2	9.7
		Olbia Canyon	3	41.0703	9.7977	110-140	6.1 ± 1.1	3.1 ± 0.2	0.0
		Tavolara Canyon	2	40.9191	9.9023	109-160	7.5 ± 2.6	4.2 ± 0.3	11.4
		Posada Canyon	1	40.7180	9.8155	140-150	9.5 ± 2.9	6.1 ± 0.5	0.0
	CE Sardinia (CES)	Orosei Canyon	3	40.3638	9.8949	95-188	11.1 ± 2.3	2.8 ± 0.1	0.0
		Cala Gonone Canyon*	1	40.2891	9.6638	134	1.2 ± 1.2	2.2 ± 0.5	0.0
		Arbatax Canyon*	1	39.9681	9.7281	108-140	0.4 ± 0.4	2.3 ± 1.8	0.0
	SE Sardinia (SES)	Palmeri Cape	2	39.6238	9.6811	96-120	8.1 ± 1.9	2.2 ± 0.1	12.6
		Porto Corallo	4	39.3787	9.6852	85-135	11.1 ± 2.1	4.5 ± 2.9	3.9
		Villasimius Canyon*	2	39.0607	9.5489	124	1.9 ± 1.5	2.4 ± 0.4	0.0
	South Sardinia (SS)	Boi Cape	6	39.1104	9.4290	90-140	15.1 ± 2.8	3.6 ± 0.1	14.1
		Nora Canyon	1	38.7387	9.1016	50-80	8.0 ± 2.4	3.0 ± 0.2	0.0
	SW Sardinia (SWS)	Teulada Cape	3	38.6882	8.4909	114-140	2.6 ± 0.9	6.7 ± 0.8	0.0
		Toro Is.	3	38.8445	8.4166	80-120	17.3 ± 3.9	5.6 ± 0.1	33.3
		St. Pietro Is.	7	38.9969	8.1287	75-160	7.9 ± 1.4	5.4 ± 0.2	14.1
		Punta delle Oche	3	39.2416	8.2836	75-90	23.6 ± 5.2	5.7 ± 0.1	8.3
ST	Campanian Archipelago (CA)	Ischia	7	40.6912	13.8939	53-128	25.2 ± 2.2	8.0 ± 0.1	11.8
		Gulf of Naples	7	40.7729	14.1516	96-134	1.9 ± 0.3	4.0 ± 0.3	48.9
		Gulf of Salerno	8	40.5763	14.4282	53-115	8.6 ± 1.3	5.5 ± 0.1	13.1
	Tyrrhenian Calabria (TC)	Cetraro*	1	39.4376	15.9288	143	0.2 ± 0.1	5.5 ± 1.5	0.0
		Gulf of St. Eufemia	11	38.7696	16.1303	7 -150	0.6 ± 0.1	4.7 ± 0.3	0.0
		Vaticano Cape*	1	38.6977	15.7468	140	0.3 ± 0.1	4.0 ± 0.6	100.0
		Palmi	3	38.3662	15.8387	50-105	8.5 ± 2.5	5.3 ± 0.2	0.5
	Messina Strait*	Messina Strait*	4	38.2579	15.7139	55-220	0.6 ± 0.3	4.1 ± 0.4	0.0
	North Sicily (NS)	Rasocolmo Cape*	1	38.3534	15.5333	180-195	0.1 ± 0.1	5.0 ± nd	0.0
		Milazzo Cape	4	38.2831	15.2465	82-110	8.8 ± 2.6	4.3 ± 0.1	50.6

(Continued)

TABLE 1 Continued

Macroarea	Coral area	Locality	n° Sites	Lat	Long	Depth range (m)	Av. Density ± SE	Av. Height ± SE	Ent. (%)
		Gulf of Patti*	1	38.1854	15.0402	59	0.3 ± 0.3	3.6 ± 0.4	0.0
	Aeolian Archipelago*	Panarea Is.*	1	38.6749	15.1267	90	0.2 ± 0.2	2.0 ± nd	0.0
		Vulcano Is.*	2	38.7098	14.9747	72-110	0.3 ± 0.2	11.6 ± 2.5	0.0
	Offshore St. Vito (OS)	St. Vito Cape	3	38.1907	12.7712	80-106	2.1 ± 1	3.4 ± 0.4	0.0
		Scuso Bank*	2	38.2211	12.5561	113-132	0.3 ± 0.1	4.8 ± 0.7	55.6
	Egadi Archipelago*	Levanzo Is.*	2	38.0470	12.4325	76-110	1.0 ± 2.4	2.7 ± 0.3	0.0
SC	Offshore banks (OB)	Graham Bank	3	37.3722	12.7948	120-161	4.9 ± 1.3	9.6 ± 0.2	0.4
	Pelagie Archipelago (PeA)	Pantelleria Is.	4	36.8262	12.0127	86-150	1.0 ± 0.4	3.8 ± 0.4	22.9
	South Sicily (SoS)	Ragusa Bank	1	36.6525	14.4869	80-93	15.5 ± 1.8	8.9 ± 0.3	39.9
SEAM	Tyrrhenian seamounts*	Vercelli Smt.*	1	41.1403	10.9044	111	0.1 ± 0.1	12.0 ± nd	0.0
		Palinuro Smt.*	2	39.4861	14.8384	121-195	1.1 ± 0.5	12.2 ± 1.3	0.0

*Coral areas and localities with less than 30 colonies counted in the frames.

Results

Occurrence and structure of the red coral forests

Red coral populations were present in 170 of the 624 sites considered in this work, corresponding to 27.2% of the total. The sites in which less than 30 colonies were counted were excluded from the quantitative analysis regarding the identification of coral areas, including the seamounts populations, represented by a limited number of colonies (Table 1 and Figure 1). Based on the geographic proximity of the remaining sites, 37 localities with red coral were identified. These were grouped into 17 distinct coral areas based on their topographic and oceanographic affinity, all belonging to the four identified coastal macro-areas. These areas were represented by 84.1% of the investigated sites and included about 99% of the counted colonies.

The average density between the 17 coastal coral areas varied between 1.0 ± 0.4 colonies m^{-2} in the Pelagie Archipelago (namely Pantelleria Island) and 23.8 ± 3.2 colonies m^{-2} on the Portofino Promontory (Table 1 and Figure 2A). Significant differences were observed among densities in the different coral areas (Kruskal-Wallis, $p < 0.0001$, Hc = 311.1) (Figures 3A–C). In the Ligurian Sea, average densities were relatively low in the western sector, ranging between 6.6 ± 1.2 colonies m^{-2} in the Sanremo area and 12.8 ± 2.3 colonies m^{-2} in the Savona area, in comparison to the eastern one (Figure 2A). Nevertheless, in the Savona area were recorded the maximum values of density of the entire dataset, namely 122 colonies m^{-2} on the Maledetti Shoal. In the North-central Tyrrhenian Sea, the Tuscan Archipelago and South Sardinia showed significantly higher average densities (19.4 ± 1.4 colonies m^{-2} and 14.1 ± 2.5 colonies m^{-2}, respectively) (Figures 2A, 3B, C). The localities

showing the highest average densities were Elba Island for the Tuscan Archipelago, Ponza Island for the Pontine one, and Caprera Canyon, Orosei Canyon and Porto Corallo for the eastern Sardinian coast (Table 1 and Figure 3D). Along the South and South-West coast of Sardinia, instead, maximal values were recorded in Boi Cape and Punta delle Oche (Figure 3C), reaching densities comparable to the one of the Portofino Promontory (Table 1).

In the South Tyrrhenian Sea, the densest populations were observed in the Campanian Archipelago and on Milazzo Cape, with 11.8 ± 1.1 colonies m^{-2} and 8.8 ± 2.6 colonies m^{-2}, respectively (Figure 2A). In this macro-area, Ischia Island (Campania) and the Milazzo Promontory reached also the highest maximal values (Table 1). The Tyrrhenian Calabrian coast and the sites offshore St. Vito showed very scattered populations (Table 1 and Figures 2A, 3A). Finally, in the Sicily Channel, the South Sicily area (Ragusa Bank) showed the highest average density (15.5 ± 1.8 colonies m^{-2}) with respect to offshore banks (Graham Bank) and Pelagie Archipelago (Pantelleria Island) (Table 1 and Figure 2A). Nonetheless, also this macro-area was overall characterized by scattered populations.

In general, in terms of average height, the investigated coral areas showed a small range of variation, with two significantly higher peaks, both recorded in the Sicily Channel macro-area, namely the offshore banks (9.6 ± 0.2 cm) and South Sicily (8.9 ± 0.3 cm) (Kruskal-Wallis, $p < 0.0001$, Hc = 2461) (Table 1 and Figures 2B, 3E–I). In the Ligurian Sea, the Maledetti Shoal (Savona) and Punta del Faro (Portofino Promontory) showed the highest average and maximal heights, with colonies reaching up to 20 cm (Table 1). In the North-central Tyrrhenian Sea, the average colony height varied between 2.8 ± 0.1 cm in CE Sardinia and 5.6 ± 0.1 cm in SW Sardinia. Maximal heights were mainly recorded in S and SW Sardinia, up to 25 cm (Boi Cape) (Table 1 and Figures 2B, 3H). In the South
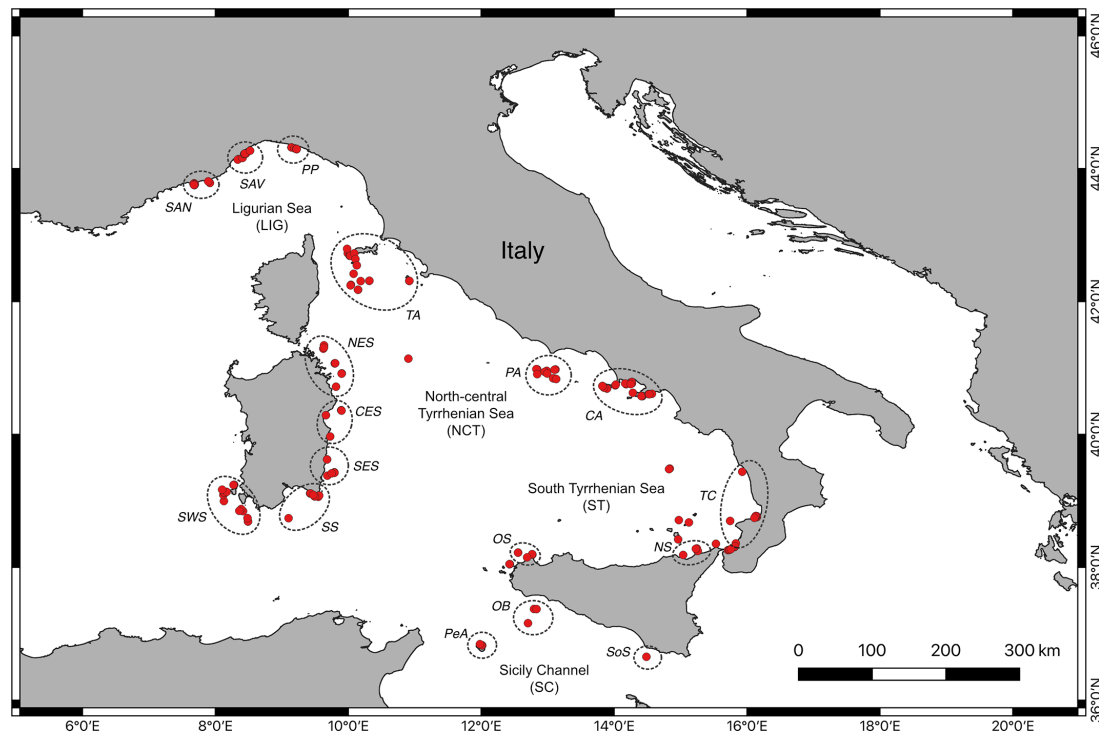
Map of the study area with location of the sites with red coral (red dots) grouped per coral area (dashed circles). For coral areas' codes, refer to Table 1.

Tyrrhenian Sea, a significant peak was recorded in the Campanian Archipelago, where the average height of the colonies was 7.1 ± 0.1 cm (Figure 2B). In this latter coral area, high maximal heights were recorded in all localities (Table 1). No significant correlation was found within the dataset between average height and average density of the colonies (r = 0.2236, graph not shown).

The size-frequency distributions, calculated for the coral areas, were generally skewed towards the small size classes with a long tail of large colonies (Figure 4). The modal classes were generally found in the 2-4 cm size classes for the western Ligurian Sea, Pontine Archipelago, E Sardinia, SW Sardinia and North Sicily. The modal classes were slightly shifted in the 4-6 size classes in the eastern Ligurian Sea, Tuscan Archipelago and Tyrrhenian Calabria. The populations measured in the Campanian Archipelago and in the Sicily Channel showed a more symmetric distribution characterised by a positive kurtosis and a modal class between 6 and 10 cm. In addition, a second mode of larger colonies was found in the western Ligurian Sea (6-10 cm, mainly attributed to the Savona coral area), in the Pontine Archipelago (6-8 cm, mainly attributed to Zannone Island), in the Tyrrhenian Calabria (8-10 cm, mainly attributed to Palmi), and in the Sicily Channel (12-14 cm, mainly attributed

to Graham Bank) (Figure 4). Very large colonies were extremely rare: on a total of 15549 measured colonies, only 25 (0.16%) exceeded 20 cm height. These were located in the Ligurian Sea, Tuscan Archipelago, E and SW Sardinia, and in the Campanian Archipelago.

The two seamounts where *C. rubrum* was present (Vercelli and Palinuro) showed very low average density values (0.1 ± 0.1 colonies m^{-2} and 1.1 ± 0.5 colonies m^{-2}, respectively). The few colonies encountered on the Palinuro Seamount (Figure 3I) measured up to 20 cm (Table 1).

The influence of depth and latitude on the density and size of red coral forests

Considering clustered data according to depth ranges, the populations average density resulted inversely related to depth (Figure 5A), ranging from an average value of 18.6 ± 2.0 colonies m^{-2} in the first depth range to 0.4 ± 0.1 colonies m^{-2} in the deepest one (Kruskal-Wallis, p < 0.0001, Hc = 31.18). On the deepest part of the continental shelf (40-80 m), the three density categories were all largely represented (32.7-34.7%), while, with increasing depth, populations were constituted by a higher
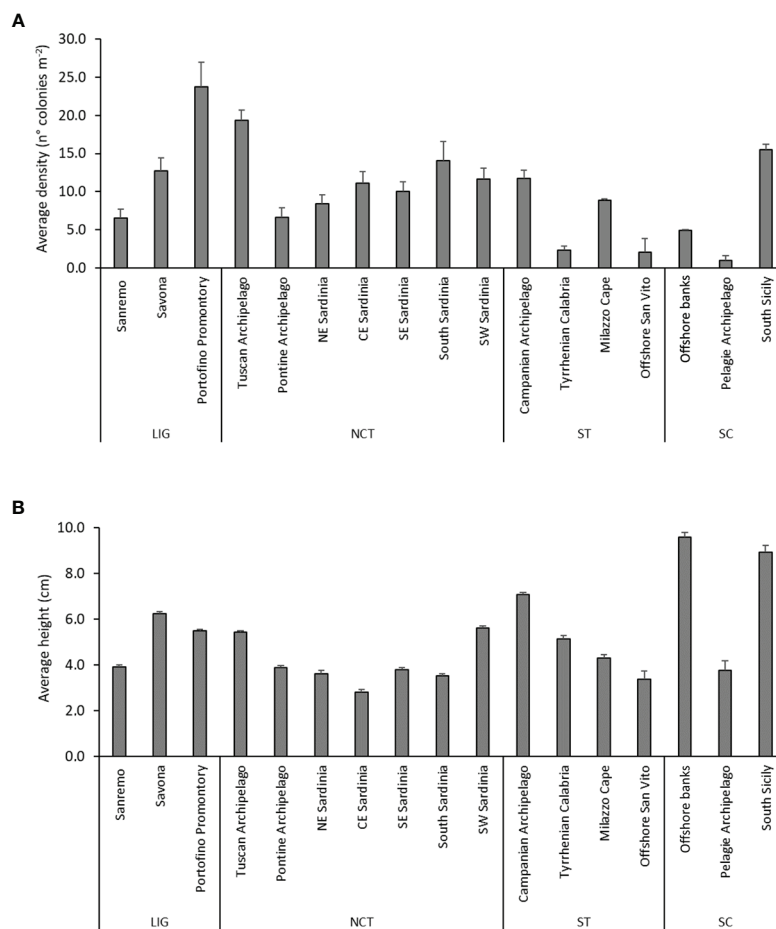
FIGURE 2
Demographic characteristics of the coral areas. **(A)** Average density ($\pm$ SE) and **(B)** average height ($\pm$ SE) of the populations in the 17 identified coral areas.

percentage of populations dominated by scattered colonies, which became the only represented category at bathyal depths (> 200 m) (Figure 5B). No clear depth-related pattern was observed for the colony average size between the clustered depth ranges, varying between a minimum of 4.2 $\pm$ 0.1 cm at 80-150 m and a maximum of 6.0 $\pm$ 0.1 cm below 200 m. Differences among average height values tested significant only for the 80-150 m depth range (Kruskal-Wallis, $p < 0.001$, Hc = 15.79, graph not shown).

The average density of the red coral populations clustered per macro-area showed a strongly significant decreasing pattern with depth, with a maximal value registered in the Ligurian Sea (13.8 $\pm$ 1.4 colonies m^{-2}) (Figure 5C). The minimal values were, for the coastal macro-areas, 4.3 $\pm$ 0.8 colonies m^{-2} in the Sicily Channel, and 0.8 $\pm$ 0.3 colonies m^{-2} on the offshore seamounts. On the contrary, a strongly significant correlation was recorded between average colony height and depth in the considered

macro-areas, with a peak in the Sicily Channel (8.9 $\pm$ 0.2 cm) for coastal macro-areas, and on offshore seamounts (12.2 $\pm$ 1.2 cm) (Figure 5D).

Fishing impact

In total, 17.5% of the counted colonies considered in the site selection were entangled in abandoned, lost or otherwise discarded fishing gear (ALDFG), including nets and longlines (Figures 6A–D). Considering the macro-areas, the Ligurian Sea was the one showing the overall highest percentage of entanglement, varying between 24.7% on the Portofino Promontory and 40.8% in the Sanremo area, with a peak in the Bordighera Canyon (78.7%) (Table 1 and Figure 7A). The southern macro-areas followed with single coral areas showing even higher peaks of percentage entanglement than those
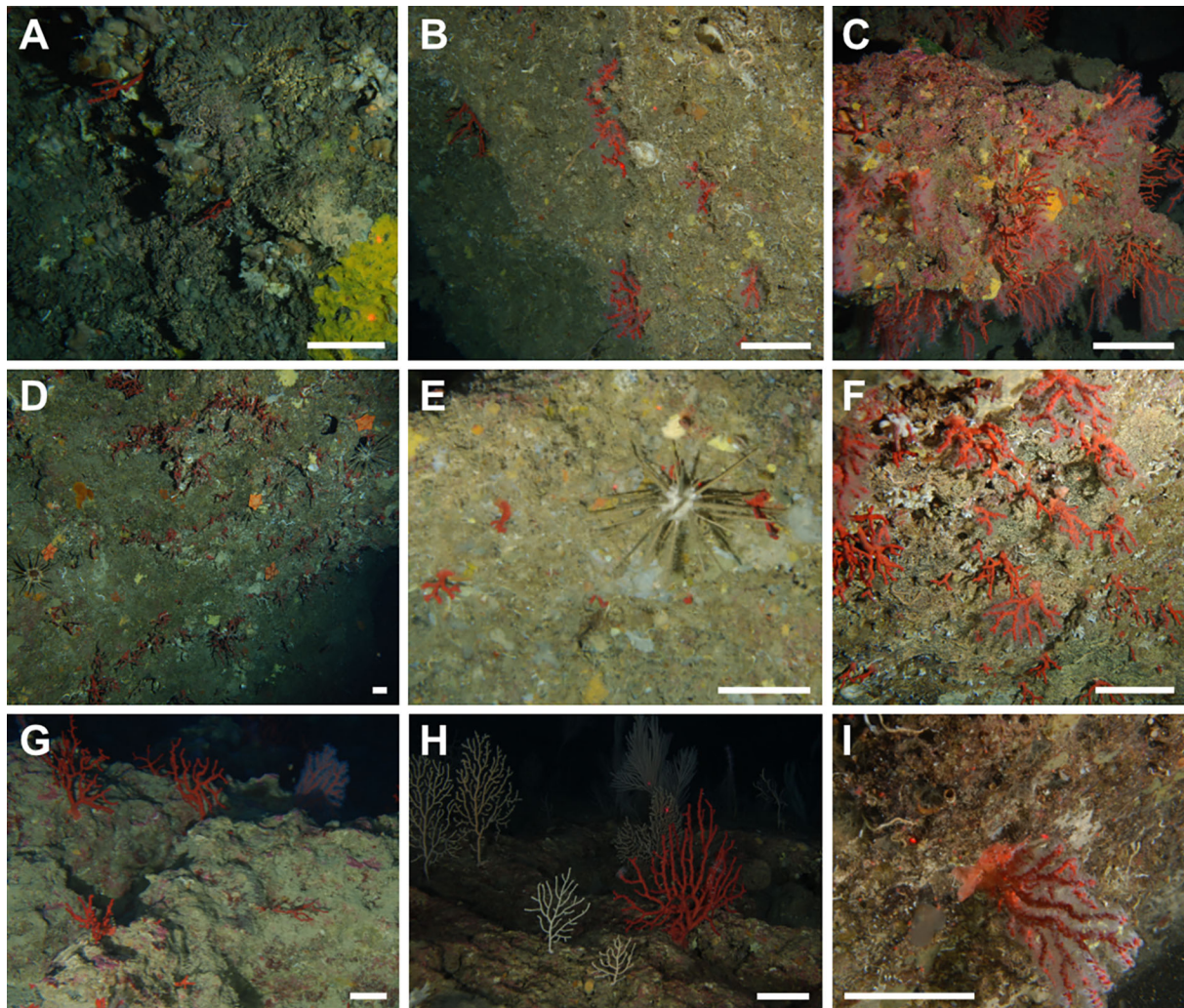
FIGURE 3

Corallium rubrum aggregations. **(A)** Scattered colonies on a vertical cliff in Palmi (Tyrrhenian Calabria, 85 m); **(B)** vertical rocky wall hosting aggregated colonies of *C rubrum* in Giglio Island (Tuscan Archipelago, 100 m); **(C)** very dense aggregation of red coral on a sloping CCA-covered rock in Punta delle Oche (SW Sardinia, 85 m); **(D)** *Peltaster placenta* (Müller & Troschel, 1842) and *Stylocidaris affinis* (Philippi, 1845) feeding on a dense aggregation of small living and dead colonies of *C rubrum* (Porto Corallo, SE Sardinia, 95 m); **(E)** very small colonies predated by *S. affinis* (Montecristo Island, Tuscan Archipelago, 84 m); **(F)** medium-size red coral colonies coexist with the white scleractinian *Thalamophyllia gasti* (Döderlein, 1913) on the vertical cliffs of Boi Cape (South Sardinia, 108 m); **(G)** large colonies flourish on the sub-horizontal CCA-covered rocks in the Ragusa Bank (Sicily Channel, 85 m); **(H)** a large colony surrounded by *Eunicella cavolini* (Koch, 1887) and *Callogorgia verticillata* (Pallas, 1766) (Capo Teulada, SW Sardinia, 124 m); **(I)** a single large colony of the precious coral hanging from a vertical rocky cliff on the Palinuro Seamount (121 m). Scale bar: 10 cm.

identified in the Ligurian Sea, such as Milazzo Cape (North Sicily, 50.6%), Ragusa Bank (South Sicily, 39.9%), and Pantelleria Island (Pelagie Archipelago, 22.9%). The North-central Tyrrhenian macro-area overall showed the lowest percentages, ranging from 6.4% (NE Sardinia) to 17.7% (SW Sardinia). Few coral areas showed a very negligible percentage of entanglement (below 0.5%) (Table 1 and Figure 7A).

An inverse relationship between the average percentage of entangled colonies and depth was found, with the deepest populations being the less impacted (Kruskal-Wallis, p = ns, Hc = 5.34) (Figure 7B). The average percentage entanglement ranged from $16.0 \pm 2.3\%$ for the populations found along the deepest part of the continental shelf (40-80 m) to virtually absent for those at bathyal depths (>200 m).

The average percentage entanglement of the red coral colonies clustered per macro-area showed a strongly significant decreasing pattern with depth, with offshore seamount populations free from fishing impact (Figure 7C).
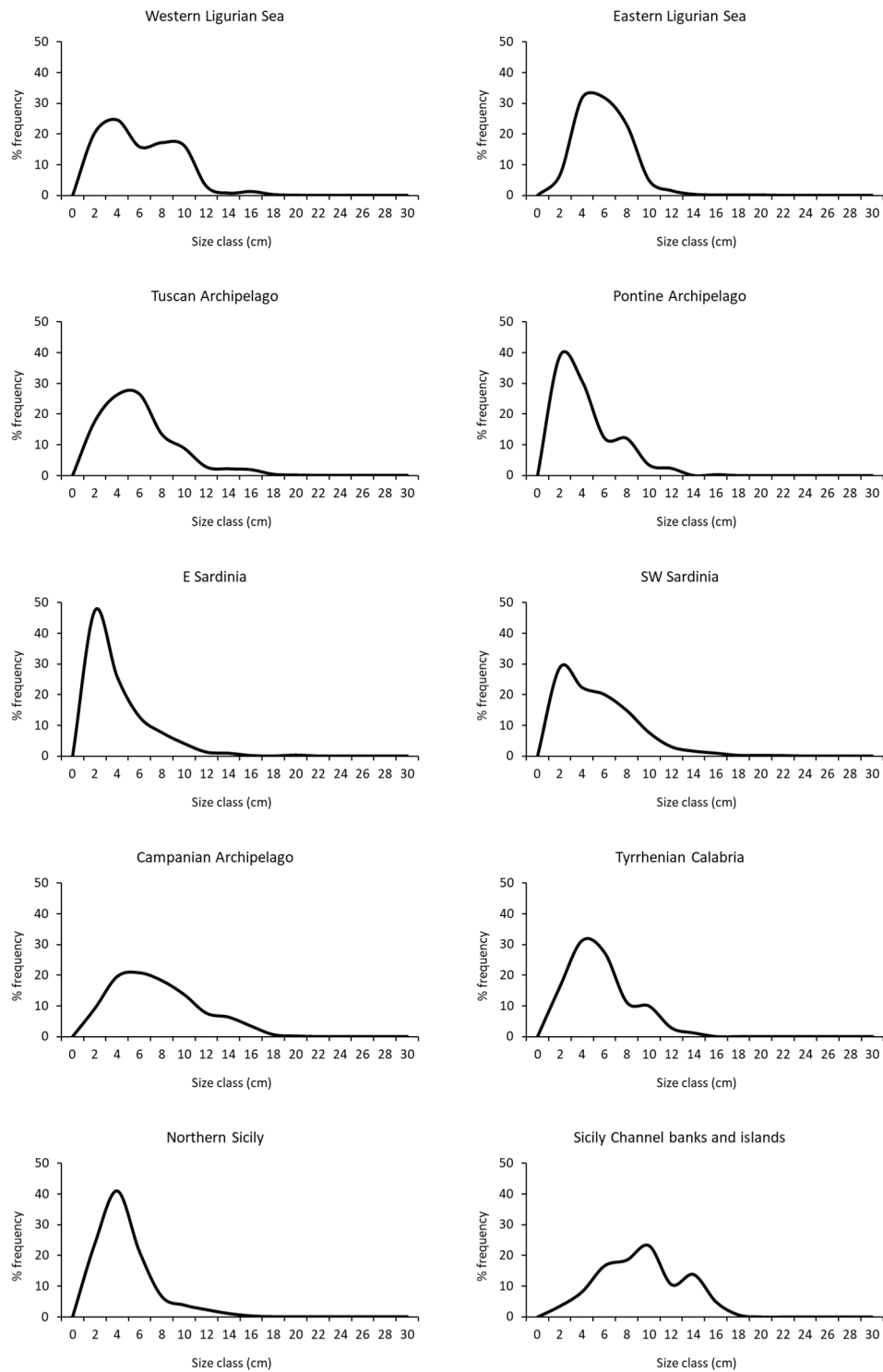
FIGURE 4
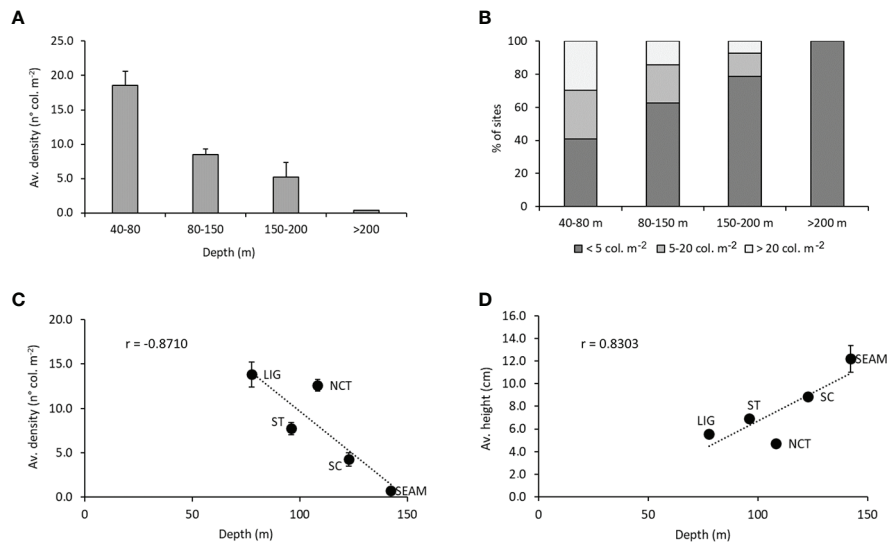Size-frequency distribution of the populations in the coral areas.

FIGURE 5
Bathymetric and latitudinal effect. **(A)** Relationship between average density (± SE) of the populations and depth in the four considered depth ranges. **(B)** Percentage of sites with scattered populations (dark grey), dense populations (grey), and very dense populations (light grey) in the four depth ranges. **(C)** Correlation between average density (± SE) of the populations grouped per macro-area and depth. **(D)** Correlation between average height (± SE) of the populations grouped per macro-area and depth.
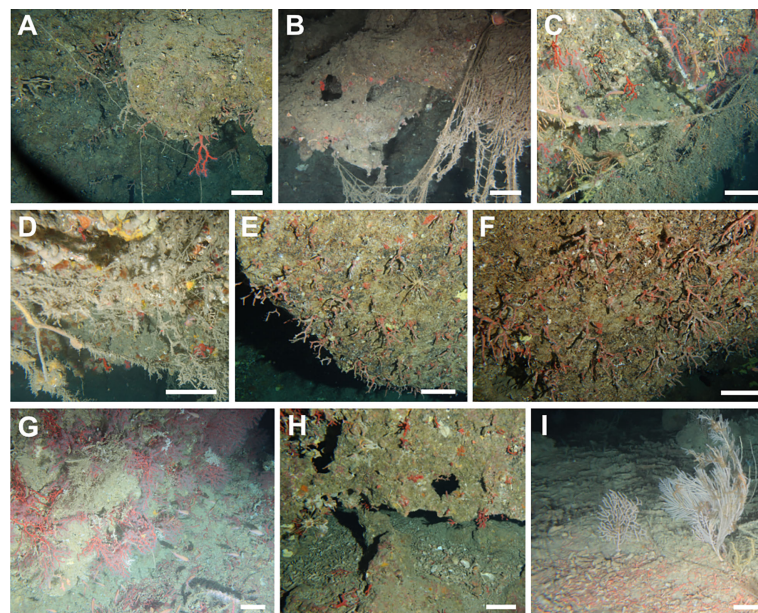

FIGURE 6
Fishing impact and mass mortalities. **(A)** Living and dead colonies entangled with a longline (Gulf of Salerno, 98 m); **(B−D)** nets impacting on *Corallium rubrum* (Milazzo Cape, 110 m; Ischia Island, 70 m; Bordighera Canyon, 70 m, respectively); **(E, F)** extensive mass mortality on the vertical rocky cliffs in Boi Cape (South Sardinia, 118 m); **(G)** large patch of coral fragments beneath flourishing living colonies (Graham Bank, Sicily Channel, 147 m); **(H)** coral fragments at the base of a rocky boulder hosting living and dead colonies (Porto Corallo, SE Sardinia, 87 m); **(I)** dense patch of *C. rubrum* fragments in the detritus (Graham Bank, Sicily Channel, 80 m). Scale bar: 10 cm.
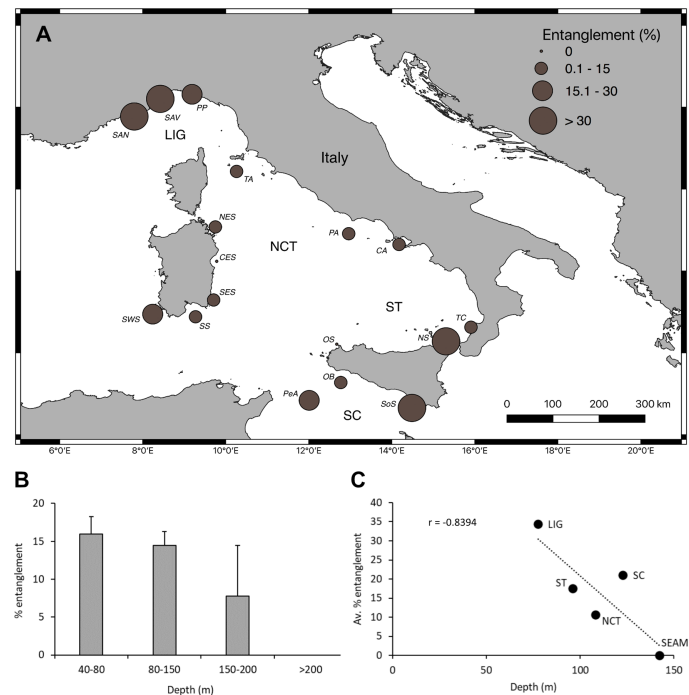
FIGURE 7
Fishing impact. **(A)** Map of the coral areas showing evident traces of impact (entanglement) by nets and longlines. The size of the dots refers to the average percentage of entanglement. **(B)** Relationship between the average percentage of entangled colonies and depth in the four depth ranges. **(C)** Correlation between the average percentage entanglement per macro-area and depth.

Deep mass mortalities

In 30 of the explored sites (17.6%), large patches of dead colonies still in place, ascribed to mass mortality events, were observed at mesophotic and upper bathyal depths (70-198 m, with the maximum recorded in the Caprera Canyon, NE Sardinia) (Table 2). 25 of these sites presented both living and dead populations, while 5 presented exclusively dead colonies. In addition, 8 sites showed no dead colonies in place on the hardgrounds, but detectable large patches of coral rubble on the nearby detritic seafloor. These latter sites were found between 80 m and 160 m along the southern Sardinian coast and were often located nearby living populations (Table 2 and Figures 6G–I).

Mass mortality events were mainly recorded in Sardinia Island (57% of the sites with dead colonies), particularly in Boi Cape (S Sardinia, 5 sites, between 90 m and 140 m), and in Porto Corallo (SE Sardinia, 4 sites, between 85 m and 135 m) (Table 2 and Figures 6E, F). Another coral area particularly impacted by these events was the Campanian one: dead populations were recorded in the Gulf of Naples (96-134 m) and in the Salerno Gulf (70-115 m). Large dead patches of red coral were found also in the Pontine Archipelago (110-193 m) and along the North Sicilian coast, including the Aeolian Archipelago (107-128 m)

(Table 2). Dead in-place patches were absent in the Ligurian Sea, in the Sicily Channel and on seamounts. Considering both living and dead colonies in the 9 involved coral areas, it was possible to report an incidence of mortality of less than 50% of the colonies in one-third of the populations, between 50 and 75% in about one-fifth of the populations and between 75 and 100% in the remaining 44% of the populations. Mass mortality events interested populations settled on vertical hardgrounds, including outcropping rocks (19 sites) and rocks covered by CCA (11 sites) (Figures 6E–I).

The overall density and height comparison between living and dead colonies, when co-occurring, showed no differences (an average density of about 9 colonies m^{-2} and an average height of about 4 cm). Nevertheless, locally, some differences were recorded in terms of density (Figure 8). In particular, 14 sites, corresponding to 57% of the sites where both living and dead colonies were simultaneously present, showed a higher density of dead colonies with respect to living ones, with the maximum average density (55.6 ± 9.6 colonies m^{-2}) recorded in Boi Cape (Figure 8).

Dead colonies occasionally suffered from a secondary direct impact from lost fishing gear. Traces of entanglements, visible on up to 52% of the colonies (Teulada Cape, SW Sardinia), were found in 33% of the sites with mortality events (Table 2).

TABLE 2 Red coral mass mortalities.

Macroarea	Coral area	Locality	Site Code	Depth range (m)	Av. Density ± SE	Av. Height ± SE	Ent. (%)	Subst.	Av. Slope (°)
NCT	Pontine Archipelago (PA)	Ponza Is.	PO16*	116-160	5.3 ± 2.0	3.1 ± 0.3	0.0	C	87.0
			PO17*	155-193	3.6 ± 1.6	3.5 ± 0.3	0.0	R	83.0
			PO19*	110-120	5.1 ± 1.6	3.0 ± 0.2	38.7	R	87.5
	NE Sardinia (NES)	Caprera Canyon	SNE9	175-198	9.7 ± 3.1	3.5 ± 0.3	0.0	R	71.0
	CE Sardinia (CES)	Orosei Canyon	SCE1*	95-115	0.7 ± 0.3	5.0 ± 0.0	0.0	R	71.0
			SCE2*	100	0.7 ± 0.3	5.0 ± 0.0	0.0	R	69.5
		Arbatax Canyon	SCE6*	108-140	6.9 ± 2.9	4.5 ± 0.2	0.0	R	89.0
	SE Sardinia (SES)	Porto Corallo	SSE5*°	122-135	13.6 ± 2.6	3.8 ± 0.2	28.7	R	90.0
			SSE6	112-135	24.1 ± 3.8	4.1 ± 0.1	0.0	R	90.0
			SSE7*	100-127	14.8 ± 3.5	2.6 ± 0.2	0.0	C	90.0
			SSE9*	85-105	10.5 ± 2.7	3.3 ± 0.1	0.0	C	90.0
	South Sardinia (SS)	Boi Cape	SSB1*	115-135	11.9 ± 1.8	2.8 ± 0.1	0.0	C	90.0
			SSB4*	117-118	55.6 ± 9.6	4.5 ± 0.1	0.0	R	90.0
			SSB5*	108-115	22.8 ± 6.3	1.9 ± 0.1	0.0	R	90.0
			SSB6*	90-124	6.1 ± 1.4	3.7 ± 0.3	1.4	C	90.0
			SSB7*	93-140	0.6 ± 0.3	5.0 ± 0.0	0.0	C	90.0
	SW Sardinia (SWS)	Teulada Cape	SSW2*	135-140	18.1 ± 4.8	2.8 ± 0.2	51.9	R	90.0
			SSW9*°	110-120	6.6 ± 0.9	4.7 ± 0.2	6.4	R	89.0
		St. Pietro Is.	(SSW12)	155-160					
		Toro Is.	SSW16*	120-125	0.5 ± 0.2	5.0 ± 0.0	0.0	R	89.0
		Punta delle Oche	SSW25*	85-90	2.4 ± 0.9	4.6 ± 0.8	0.0	C	89.0
ST	Campanian Archipelago (CA)	Gulf of Naples	GNM3*	96-124	5.3 ± 1.1	6.5 ± 0.5	39.1	R	90.0
			GNM5*	120-134	0.3 ± 0.2	5.0 ± 0.0	0.0	R	90.0
			GNM6	120-130	0.6 ± 0.2	5.0 ± 0.0	0.0	R	89.0
			GNM12*	110-120	3.7 ± 0.9	4.5 ± 0.5	71.0	R	90.0
		Gulf of Salerno	GS2*	70-105	12.3 ± 1.5	7.1 ± 0.3	15.4	C	90.0
		Li Galli	GS3*	91-115	17.0 ± 2.7	7.9 ± 0.3	0.0	C	90.0
			GS4*	91-98	11.2 ± 1.9	5.9 ± 0.3	8.9	C	90.0
		Amalfi	GS9*	95-102	0.6 ± 0.2	5.0 ± 0.0	0.0	R	89.0
	North Sicily (NS)	Milazzo Cape	MI8	90-100	3.0 ± 1.0	4.1 ± 0.2	37.1	R	90.0
	Aeolian Archipelago	Alicudi Is.	EO26	107-128	3.2 ± 1.4	4.9 ± 0.4	0.0	C	90.0
SC	Offshore banks (OB)	Graham Bank	(BCS11)°	137-147					
			(BCS12)°	150					
			(BCS16)°	120-125					
			(BCS17)°	100-120					
			(BCS20)°	80					

Sites are grouped per locality, coral area, and macro-area. Depth range, average density and height, entanglement, substrate, and average slope of the dead populations are presented. *Sites where both dead and living populations were observed. °Sites where dense patches of coral rubble were present. C, CCA-covered rocks; R, outcropping rocks.

Discussion

This work considered the widest demographic dataset ever produced on *Corallium rubrum*, with a specific focus on the mesophotic and upper bathyal depths of the Italian coast. This species confirms to be widespread in the basin, with seventeen coral areas identified based on their geographic proximity and topographic and oceanographic affinity. Among them, some
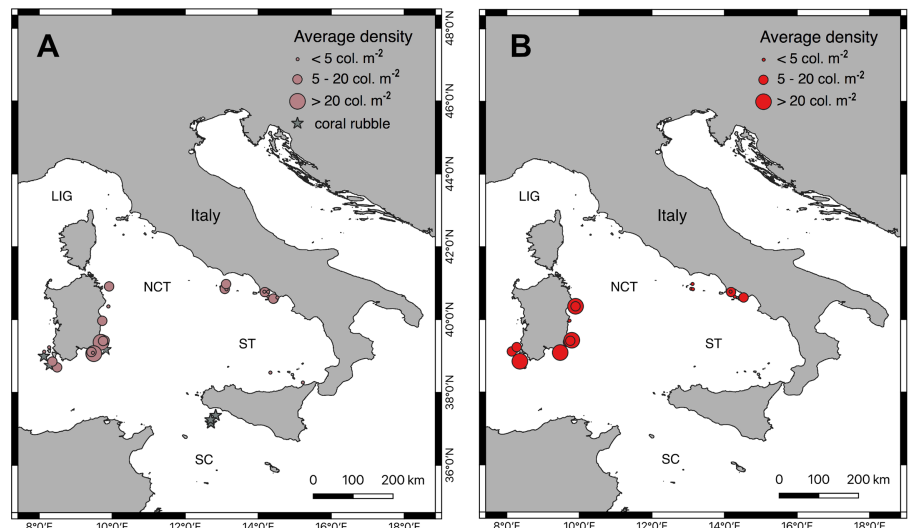
FIGURE 8
Deep mass mortalities. Comparative maps of the sites where dead **(A)** and living **(B)** colonies were observed. The size of the dots refers to the average density of the populations. Grey stars indicate the sites where patches of coral rubble were visible in the sediment.

showed high density and considerable size of the colonies (such as those of the Portofino Promontory, Tuscan Archipelago, South and South-western Sardinia, Campanian Archipelago and South Sicily), representing important larval stock for the species, and these may be the target of specific management actions as required by the most recent species and habitat regional assessments (Otero et al., 2017; Montefalcone et al., 2021).

In general, the investigated populations consistently showed a size-frequency distribution skewed towards small-size colonies, with low variability among the areas and among depth ranges. Although it is recognized the possibility of a limited bias in the measures obtained through bidimensional ROV footage with respect to the ones derived by three-dimensional techniques (Lagudi et al., 2022), the overall patterns appear clear. The size of colonial organisms such as *C. rubrum* is known to be potentially locally constrained by numerous environmental parameters (e.g., food and substrate availability, temperature, currents, depth, slope) (e.g., Cau et al., 2016; Galli et al., 2016) as well as by anthropic pressures, mainly harvesting and fishing (e.g., Tsounis et al., 2006; Rossi et al., 2008; Bruckner, 2009; Cattaneo-Vietti et al., 2016). Over the spatial scale here considered, these factors may be synergically responsible for the recorded variations, especially when considering the occurrence, in certain coral areas (western Ligurian Sea, Pontine Archipelago, Tyrrhenian Calabria, Sicily Channel), of multiple cohorts of colonies. However, overall, it seems that, among all factors, depth does not influence the size of the colonies. This is in accordance with Carugati et al. (2022),

reporting no significant variation of colony height with depth in the North-western Sardinian populations (50-290 m), but contrasts with the findings of other authors sustaining the major size (as well as diameter and branching) of deep-dwelling colonies, a trend mainly attributed to a lower harvesting pressure (e.g., Tsounis et al., 2007; Rossi et al., 2008; Priori et al., 2013; Angiolillo et al., 2016; Cau et al., 2016). Moreover, the same authors provided evidence of a size/density relationship within *C. rubrum* populations, with larger, but more scattered colonies in deeper waters, that did not result from the present dataset.

Together with indeed ecological considerations, the homogeneous reduced size of the red coral populations in the entire study area could be related also to a stressful situation due to the long-term harvesting pressure carried out in all the considered basins (Cattaneo-Vietti et al., 2016). Already Bruckner (2009, 2014), based on data derived from the landed harvested material, supported the use of size reduction in time as the main indicator of the harvesting impact on the demography of the populations. Similar conclusions were also derived from *in-situ* local studies, carried out both on shallow and deep populations. Tsounis et al. (2006); Tsounis et al. (2007) and Rossi et al. (2008) clearly demonstrated that the harvesting pressure is the main constraint driving population structure at Cap de Creus (Spain, NW Mediterranean Sea), reporting a colony size in shallow overexploited populations noticeably smaller than that of deeper, less harvested populations (average colony size: 3.0 ± 1.7 cm, and 7.8 ± 3.3 cm, respectively, in shallow and deep populations). Significant

differences in terms of basal diameter and maximum height emerged from the comparison between harvested and non-harvested populations around Marseilles (France) (Garrabou and Harmelin, 2002). Finally, larger colony sizes have been observed also in populations located inside protected areas, where harvesting is forbidden, as in the Medes Islands Marine Reserve (Spain) and on Ischia Island (Regno di Nettuno MPA, Campania, Italy), suggesting that the harvesting pressure has a deleterious effect on the population structure of the precious coral (Linares et al., 2010; Angiolillo et al., 2016). Our data, coming from a wide sampling effort, provide additional support to this hypothesis.

Differently from height, density is strongly driven by depth, with a linear decrease from shallow to deep sites, confirming the preliminary qualitative results obtained by Toma et al. (2022) and in accordance with known literature (e.g., Rossi et al., 2008; Carugati et al., 2022). In addition, on the continental shelf and shelf break, higher variability in terms of density was observed, with dense aggregations and populations made of sparse colonies equally present, while at bathyal depth, populations of scatted colonies were dominant. A similar pattern was already reported in Cap de Creus (North-western Mediterranean Sea) at 50-230 m (Rossi et al., 2008). The present work enhances the idea that the self-thinning process (i.e., the intra-specific competition regulating population density and structure, based on space limitations, namely hardgrounds availability) (Cau et al., 2016), is a valid explanation for the density-depth pattern observed on a large scale for *C. rubrum*, but this trend is not necessarily associated to an increase of the colonies' size with depth. It has to be considered that this latter trend of size with depth emerged from studies targeting single populations located in restricted geographic and depth ranges, and often deeply harvested since historical times in shallow waters. The present study, instead, considers a much larger area (about 680,000 m^2), and a wider depth range (from the deep circalittoral to the deep bathyal), including coastal and offshore sites subjected to a larger variety of environmental constraints and human pressures. This allowed obtaining a larger picture of the population structure of red coral, damping local influences. Interesting large-scale patterns, both in terms of density and height, emerged from the latitudinal point of view, probably related to unknown gradients of environmental (e.g., currents, temperature, silting, nutrients) and biological (e.g., competition with other co-occurring components of the assemblages) characteristics. In fact, populations showing higher densities and smaller colony heights characterize the mesophotic hardgrounds of the northern areas, with respect to the southern ones.

In terms of coastal-offshore gradient, seamounts, despite hosting only a few sparse red coral colonies generally of large size, offered some insights into the demographic trends of this species. The distance of these structures from the coast seems to act as a barrier for the larval dispersal of the species, which is generally considered on a short-medium range (Costantini et al., 2007; Martínez-Quintana et al., 2015; Costantini and Abbiati, 2016; Guizien et al., 2020). High densities of *C. rubrum* observed on other Mediterranean seamounts may be related to their closer proximity to the coast (de la Torriente et al., 2018), as well as to more favourable trophic conditions than those found on the offshore reliefs investigated here (30-70 NM from the nearest coastal populations). However, once settled, offshore red coral populations may potentially be subjected to lower levels of anthropic impact since these structures have never been interested by coral harvesting (Cattaneo-Vietti et al., 2016) and are known to have a modest fishing pressure (Bo et al., 2014), hence supporting larger sizes.

The remoteness of a site, influencing its anthropic accessibility, both in terms of depth and distance, has been considered a factor driving the demography of the red coral populations (Rossi et al., 2008). In this study, demersal artisanal and recreational fishing activities emerged as serious and widespread threats to the habitats including red coral at almost all coastal sites and depths. Colonies entangled in fishing gear were visible in almost 90% of the coral areas, with those in the Ligurian Sea and Sicily Channel being among the most impacted, and those in the Tuscan Archipelago and eastern Sardinian coast among the least. This pattern has been highlighted in numerous studies conducted on the deep megabenthic assemblages of these regions (Bo et al., 2014; Angiolillo et al., 2015; Cattaneo-Vietti et al., 2017; Cau et al., 2017). Highly impacted benthic communities have been documented along the Ligurian coast, especially in the western sector (Enrichetti et al., 2019a; Enrichetti et al., 2019b). On the contrary, the Portofino Promontory resulted among the less impacted Ligurian coral areas. This could be due to the proximity of the studied mesophotic populations to the coastal Marine Protected Area. Here, in fact, a reversion in the size-structure shift was observed by Bavestrello et al. (2015), reporting flourishing dense populations of large colonies at shallow depths after almost two decades of protection. The positive effects of restrictions on red coral populations have been reported also in North-West Sardinia, where large colonies (modal size classes 10-15 cm and 15-20 cm) were registered by Onboard Scientific Observes in catches from areas subjected to stricter harvesting measures compared to other countries within the GFCM competence area (Follesa et al., 2013; Carugati et al., 2020). This specific area within the Sardinian Sea was already reported as a hotspot of occurrence of *C. rubrum* (Toma et al., 2022). These works support the importance of MPAs and other protection measures in the conservation and management of red coral. This is particularly true if we consider the high frequency of the indirect damages of fishing activities occurring in the

deepest part of the continental shelf and along the shelf break, where the densest and more diversly aggregated populations were observed.

The present study also highlighted how, besides fishing and harvesting pressures, mass mortality events, registered down to 200 m, may represent significant stresses for mesophotic and upper bathyal red coral populations. Our data enlarge the current knowledge about red coral mass mortality events identifying a Tyrrhenian and Sicilian belt of dead red coral zones. The causes of these catastrophic events remain, however, uncertain. Similar phenomena in coastal ecosystems (0-40 m), including also red coral, have been linked to modifications in environmental conditions triggered by global changes (e.g., thermal anomalies) (Harvell et al., 1999; Cerrano et al., 2000; Pérez et al., 2000; Garrabou et al., 2001; Harley et al., 2006; Garrabou et al., 2009; Cerrano et al., 2013). However, in the deep regions where red coral mortalities have been reported, far from the influence of the seasonal thermocline, other putative causes should be addressed. For example, the red coral mass mortality event reported along the coast of Provence in 1987 (Rivoire, 1991; Arnoux et al., 1992), between 80 and 160 m, was attributed to polluted waters driven by the dominant currents in that area. The deep circulation of warm waters in proximity to volcanic areas (Bavestrello et al., 2014) combined with the seafloor movements in seismic areas (Lodolo et al., 2017; Bavestrello et al., 2021) may explain the extensive mortality events observed in the Pontine Archipelago, Campanian Archipelago and the offshore banks of the Sicily Channel. For the Sardinian sites, however, there is no clear explanation of the putative factors triggering the coral death, neither for the population along the North-eastern sector (Carugati et al., 2022) nor for those in the southern one. Most of the mortalities were recorded in submarine canyons, which may support the fact that the particular environmental conditions (e.g., turbidity currents) occurring in these systems very close to the shorelines, may have caused the events (Moccia et al., 2021). However, the co-occurrence, in the same sites, of different structuring filter-feeding anthozoans (e.g., *Antipathella subpinnata* (Ellis and Solander, 1786), *Eunicella cavolini* (Koch, 1887)) in apparently good health status would exclude a wide clogging event triggered by a massive deposition of silt (Moccia et al., 2022). Certainly, mass mortality events, both in shallow and deep waters, should be considered as additional factors significantly shaping the demography of red coral populations in the short term.

This work provides valuable information on the distribution and population structure of a precious overexploited species from a large-scale perspective. Deep coral areas, with particularly high density and size, were identified, as well as the areas most affected by fishing impact and mass mortality events. All this information is fundamental to have a comprehensive picture of the demography of an endangered species and to depict the best conservation actions.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

Conceptualization, MT, GB, MB. methodology, validation, formal analysis, MT, GB, MB. investigation, resources, data curation, writing-original draft preparation, MT, MB, GB, SC, AC, MA. writing-review and editing, MT, MB, GB, SC, AC, MA. visualization, supervision, project administration, GB, MB, SG, FA, SC. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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