



Terrain, oceanographic, and biological factors underlying the development of Mediterranean coastal animal forests

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ABSTRACT

Marine Animal Forests (MAFs) form three-dimensional seascapes and provide substrate and shelter for a variety of species. We investigated the fine-scale distribution pattern of three habitat-forming species of the coastal Mediterranean MAFs: *Eunicella cavolini*, *E. singularis* and *Paramuricea clavata*, and assessed the influence of terrain, oceanographic, and biological factors on their distribution and the formation of MAFs in the central-northern Tyrrhenian Sea. Species presence and abundance were obtained through seafloor HD imagery and were combined with terrain and oceanographic parameters extracted from remote sensing data using distance-based linear modeling (DistLM) and generalized additive model (GAM). The three studied species occurred in all the study areas, with marked differences in their abundance and distribution across the different sites and habitat type, in relation to seafloor characteristics. Specifically, positive relationships emerged between the density of colonies and terrain parameters indicative of high seafloor complexity, such as slope and roughness, as well as the number species structuring MAFs. A clear niche separation for the three species was observed: *E. cavolini* and *P. clavata* were reported on coralligenous reefs, and in areas where the seafloor complexity may enhance hydrodynamics and transport of organic matter, while *E. singularis* was observed on red algal mats at shallower depths. A better understanding of the ecology of these gorgonians, as well as of the drivers determining MAFs formation, represent the first step toward the conservation of these threatened habitats which are currently poorly protected by management and conservation plans.

1. Introduction

The habitats structured by erect megabenthic invertebrates, such as soft and hard corals, sponges, bryozoans, polychaetes, ascidians, and bivalves, are nowadays recognized as Marine Animal Forests (MAFs), reintroducing the intuitive definition coined by Alfred Russel Wallace in 1869 (Orejas et al., 2022). Over the past few decades, the technological advances in exploration and the widespread increase in the use of photo-video sampling methods significantly boosted the efforts and investigations over large areas and wide bathymetric ranges, contributing to assessing the distribution of MAFs' and defining the main structuring species (Danovaro et al., 2014; Durden et al., 2016; Rossi et al., 2021).

Such technologies allowed discovering the presence of MAFs in all world's oceans, including the Mediterranean Sea, which serves as a miniature model of the world's oceans for various aspects of marine ecology, as well as the study of MAFs (Bramanti et al., 2017).

Comprehension of the functional role that MAFs play in benthic ecological processes has increased, catalyzing the attention of the scientific community. The structural complexity of MAFs can promote important ecosystem functions and services (Graham and Nash, 2013; Paoli et al., 2017). For instance, well-developed and structured animal forests offer a multilayered habitat structure that supports high associated biodiversity (Baillon et al., 2012; Cerrano et al., 2010; Ponti et al., 2018; Sini et al., 2019); moreover, they can influence carbon storage

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(acting as carbon sinks immobilizing C in their structural molecules: Coppari et al., 2019; Rossi and Rizzo, 2020), hydrodynamic patterns (Guizien and Ghisalberti, 2017), and nutrient recycling (Rossi et al., 2017a). Suspension feeders control benthic-pelagic coupling processes, capturing seston (Rossi and Rizzo, 2021) and transferring organic matter and energy to the bottom layer, thus enhancing the biodiversity and biomass of the benthic community (Cerrano et al., 2015). The life-history traits of the species responsible for MAFs formation suggest that their functions of transfer and storage of energy and materials among different environmental compartments (*i.e.* pelagic and benthic) are provided for decades or even centuries, emphasizing the key role of these organisms in the functioning and stability of the ecosystem over time (Linares et al., 2007; Montero-Serra et al., 2018). In areas with little or no light, where photosynthetic productive processes are scarce or mainly absent, the provision of the abovementioned functions is an exclusive prerogative of heterotrophic suspension feeders (Gili and Coma, 1998).

Several anthropogenic pressures threatens the integrity of MAFs (Rossi, 2013). Climate change profoundly impacts MAFs. The increasing frequency and intensity of marine heatwaves have led to mass mortality events among coastal MAFs' structuring species (Garrabou et al., 2009, 2022; Rivetti et al., 2014), whose low resilience capacity can rapidly drive them to the brink of local ecological extinction. This has resulted in unpredicted losses in the composition and functioning of benthic ecosystems (Gómez-Gras et al., 2021b; Rossi et al., 2019). Furthermore, artisanal fishing and bottom trawling, direct harvesting, pollution, drilling, and mining affect the integrity of MAFs, jeopardizing the ecological processes and functions they provide (Angiolillo and Fortibuoni, 2020; Piazzini et al., 2021; Rossi, 2013). The rapid degradation of MAFs and global ecosystems is a concern at both the scientific and political levels (Rossi et al., 2022). This is evidenced by United Nations initiatives programmed for the decade 2021–2030, such as the UN Decade on Ocean Science for Sustainable Development (www.oceandecade.org) and the Decade of Ecosystem Restoration Declaration (www.decadeonrestoration.org), which aim to support worldwide conservation and restoration efforts.

Octocorals are among the main habitat-formers in the Mediterranean MAFs, encompassing more than 20 species that show a wide bathymetric distribution, from the infra- and circalittoral zones, down to bathyal zones (Rossi et al., 2017b). Among the octocorals, the iconic species *Corallium rubrum* (Linnaeus, 1758), *Eunicella cavolini* (Koch, 1887), *Eunicella singularis* (Esper, 1791), and *Paramuricea clavata* (Risso, 1826) form habitats of conservation interest, as defined by SPA/RAC-UN Environment/MAP (2019). Despite significant improvements in understanding the ecology and pressures impacting these species over the past two decades, we are still far from fully understanding the factors influencing the spatial distribution patterns, as well as the structure and variability of gorgonian populations. Terrain variables were taken into account in studying Mediterranean gorgonian species distribution (Bo et al., 2012; Enrichetti et al., 2019b; Gori et al., 2011; Grinyó et al., 2016; Moccia et al., 2021), but few studies considered the synergic effect of substrate features (*i.e.* terrain variables) with oceanographic (*i.e.* physico-chemical parameters of the water masses) and biological factors (*i.e.* habitat types or biocenosis as proposed by Pérès and Picard model for the Mediterranean Sea) in determining both the distribution of gorgonians, as well as the formation and composition of MAFs (Boavida et al., 2016; Blouet et al., 2022). In sessile marine invertebrates, the interaction of biological and environmental factors is responsible for patchy distribution patterns (Boudouresque et al., 2016) and spatially structured populations (Coelho et al., 2023; Karlson, 2006). Unraveling the determinants driving gorgonians' distribution and their implication in the genesis of MAFs is not obvious at all and could help prioritize conservation and management strategies.

The present study investigated at fine spatial scale the distribution of three out of the four most iconic Mediterranean octocorals (*i.e.*, *E. cavolini*, *E. singularis*, and *P. clavata*, Fig. 1) in relation to terrain,

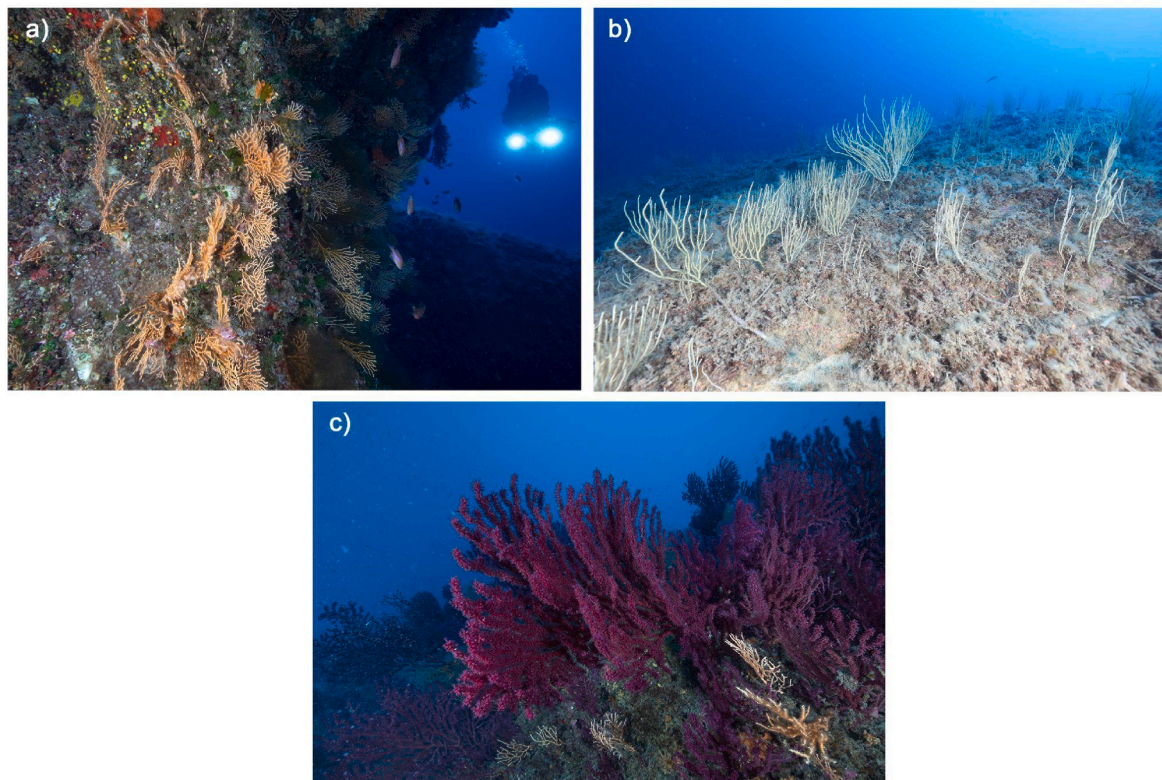


Fig. 1. General appearance of the forest seascapes provided by the three species object of the present study: *Eunicella cavolini* (a) and *Eunicella singularis* (b) at Giglio Island, *Paramuricea clavata* (c) at Costacuti bank. Photos by E. Casoli.

oceanographic, and biological features at three areas located in the central-northern Tyrrhenian Sea. The aims of the present study were to: i) quantify the occurrence and density of the three above-mentioned gorgonian species in coastal seabeds (0–50 m of depth); ii) assess the ecological requirements and the habitat selection of the species; iii) identify terrain, oceanographic, and biological factors mostly correlate with the density of colonies of the three species considered together, and therefore with the formation of monospecific and multispecific coastal MAFs.

2. Material and methods

2.1. Study areas

The study areas are located in the central-northern Tyrrhenian Sea and include: a) the western sector of the Giglio Island, b) the submerged promontory of Capo Linaro, and c) the Costacuti bank (Fig. 2). These areas are characterized by different geomorphological settings and can be regarded as exemplifying a range of environmental conditions found within the region: islands, coastal areas, and rocky banks. For each area, our work focused on four to six sites, which have been selected for video observation. The sampling strategy for site selection was planned to include a range of different depth levels and seafloor morphologies across the various areas.

Giglio Island (Fig. 2a) is the second largest island of the Tuscan Archipelago and lies 16 km off the coast. The island is mainly composed of

lower Pliocene monzogranitic intrusions whose emplacement is linked to the extensional tectonics that affected the inner sector of the Northern Apennine orogenic wedge (Rossetti et al., 2000). The coasts of Giglio Island are shaped with cliffs and small bays, and the seafloor is characterized by steep rocky slopes alternating with sandy bottoms, which host diverse and rich habitats encompassing *Posidonia oceanica* (Linnaeus) Delile, 1813 meadows, *Phyllophora crispa* (Hudson) P.S.Dixon, 1964 mats, and coralligenous reefs (Casoli et al., 2016; El-Khaled et al., 2022; Mancini et al., 2023). The island is poorly populated for most of the year, having only three small towns and a small harbor on the eastern side, and has overall low levels of anthropic pressure. It attracts a consistent flow of tourists due to its strategic geographical location: it is conveniently accessible from various Italian cities and is renowned as one of the most popular scuba diving destinations in the central Tyrrhenian Sea (Casoli et al., 2017a). Furthermore, the local artisanal fishery impacts gorgonian populations, which are often caught as by-catch (Casoli et al., 2021).

Capo Linaro promontory is located along the Tyrrhenian Italian coast about 40 km north of the Tiber River's mouth (Fig. 2b) and is mainly composed of marly calcareous and arenaceous turbidites of Meso-Cenozoic age (Bartole, 1990). The coastal submerged portions of the promontory show a complex morphology due to widespread rocky outcrops colonized by coralligenous reefs and interspersed patches of *P. oceanica* (Ardizzone et al., 2018). Coralligenous reefs are also present on scattered rocky outcrops on the sedimentary bottoms between 30 and 60 m depth (Pierdomenico et al., 2021). This area is characterized by

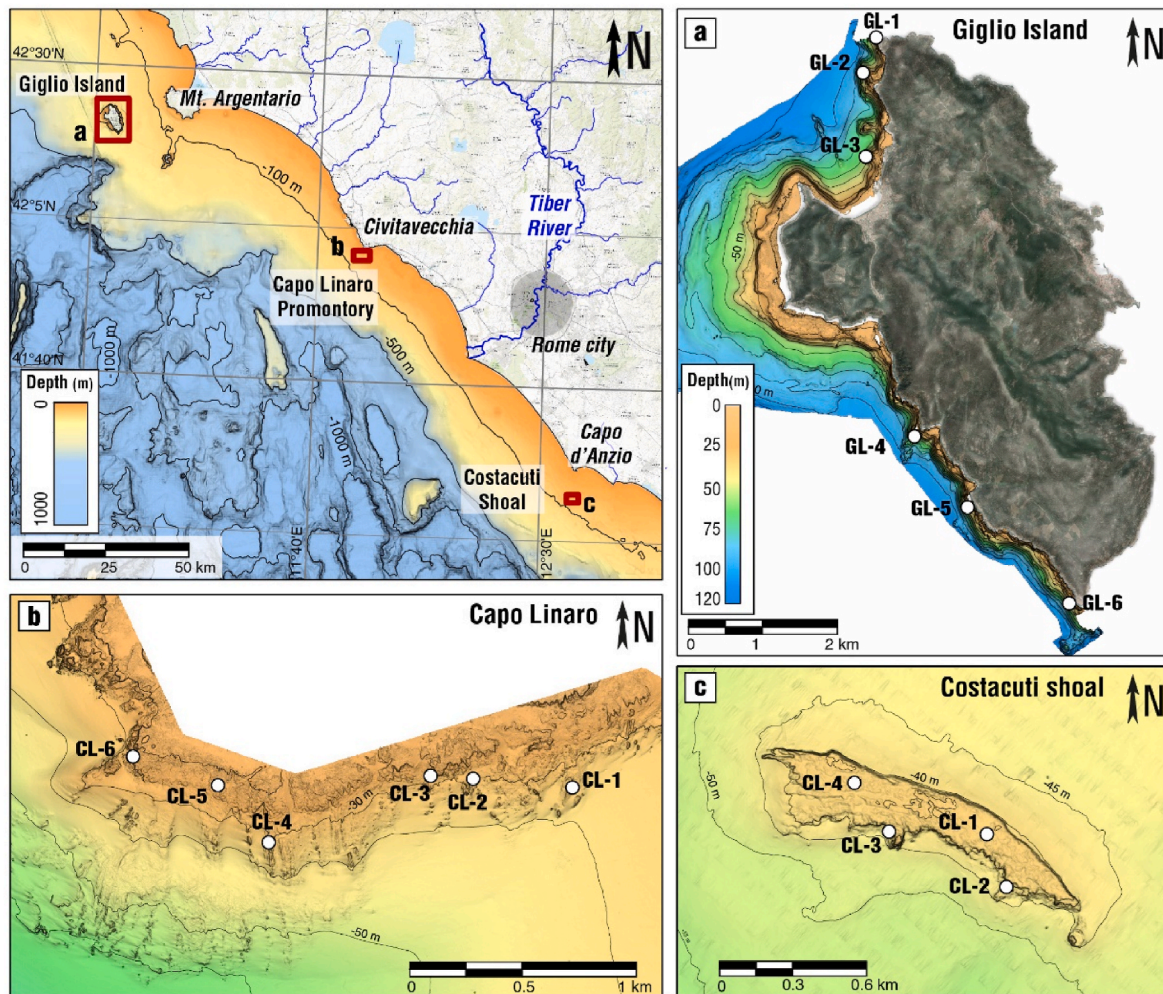


Fig. 2. Map of the study areas: Giglio Island (a – GL), Capo Linaro (b – CL), and Costacuti bank (c – CC). The dots indicate the sites where observations and data collection were carried out and their related identification codes (IDs).

enhanced sedimentation mainly related to the influence of Tiber River suspended plume (Chiocci and La Monica, 1996; Pitarch et al., 2019) and by intense hydrodynamics, due to the interaction of the submerged promontory with the prevalent northward flowing bottom currents. The main anthropogenic pressure in this area include the Port of Civitavecchia, an important hub for goods and people transportation, located about 5 km north of the Capo Linaro. The maritime traffic and harbor activities can cause impacts on coastal ecosystems such as high sediment load, re-suspension of particulate heavy metals, and organic pollution (Darbra et al., 2009). Anthropogenic pressures are also related to fishing activities carried out in the area, which can increase littering and entanglement of fishing gears on rocky substrates, along with increased sediment resuspension by trawling on adjacent sedimentary bottoms (Ferrigno et al., 2017; Consoli et al., 2019).

Costacuti is a 250 m-wide, 1500 m-long and 10 m-high isolated bank located 8 km off the coasts, in an area characterized by low sediment input from the mainland (Chiocci and La Monica, 1996; Fig. 2c). The bank, elongated in a NW-SE direction has a flat top at about 35 m depth and steep flanks (15° up to 40°) widely colonized by coralligenous reefs. A mosaic of *P. oceanica* meadows, sparse coralligenous bioconcretions, and rodoliths beds are reported on the top of the bank and on the surrounding bottoms (Nicoletti et al., 2003; Pierdomenico et al., 2021). The bank is also a frequented scuba diving spot. An intense fishing activity affects this area, as indicated by abundant fishing lines and by traces of trawls marks observed on the surroundings of the bank (Pierdomenico et al., 2021).

The hydrodynamic regime in the study areas is principally dominated by the general cyclonic Tyrrhenian circulation flowing in a SE-NW direction, with a marked seasonal variability (Astraldi and Gasparini, 1992). The variability of local hydrodynamics can also be influenced by strong wind events, coastal morphology, interaction with shallow bottoms, and freshwater inputs from torrents and rivers (Cutroneo et al., 2016).

2.2. Data collection and analysis

The general information about the biology and ecology of *E. cavolini*, *E. singularis*, and *P. clavata* are resumed in Supplementary Materials. The data used in this study to assess the presence and distribution of the three gorgonian species, along with their density, population structure, and the type of habitat they colonize include HD videos collected by Scientific Scuba Divers (SSDs) and Remotely Operated Vehicles (ROVs). Such information has been integrated with terrain and oceanographic variables extracted from bathymetric and satellite data, respectively, which have been used as predictors of the presence of MAFs.

2.2.1. Terrain variables

Bathymetric data were collected during several coastal surveys carried out between 2016 and 2017, using different Reson multibeam systems: a Seabat 7125 SV2 system (500 kHz) at Giglio Island, a SeaBat T50-P system (400 kHz) in the Capo Linaro area and a SeaBat 8125 system (455 kHz) in the Costacuti area. In all areas, the processing of raw data (for details see Casoli et al., 2017b; Pierdomenico et al., 2021) was performed to produce 2-m resolution Digital Elevation Models (DEMs). The following terrain derivatives were extracted from the DEMs using functions included in the R packages *raster* version 3.6 and *spatialEco* version 2.0: depth, slope, aspect (transformed using arcsine and represented as continuous variable ranging from -1 to 1), and terrain ruggedness (Vector Ruggedness Measure, VRM; Sappington et al., 2007), the latter calculated using a 9 × 9 m mobile window.

2.2.2. Biological variables

Optical underwater technologies were used to collect video images from which biological variables have been extracted. SSDs surveyed the western part of the Giglio Island, while different models of Remotely Operated Vehicles (ROVs, specifically Falcon and Pollux III) were used

to collect videos in the Capo Linaro and Costacuti areas, respectively. Field activities were carried out during autumn and winter of 2017 and 2018; in all surveys, both SSDs and ROVs were equipped with HD cameras (Canon 5d mark IV and GoPro Hero 5, respectively), light apparatus, parallel laser pointers (spaced 10 and 20 cm for SSDs and ROVs surveys, respectively) for scale reference, and ultra-short baseline (USBL, MicronNav) positioning system to correctly georeferencing the survey tracks. Four to six video transects were carried out at different sites in each study area, exploring a depth range between 8 and 49 m (Fig. 2 and Table 1). Sampling activities were carried out on hard bottom habitats where the three octocoral species exclusively dwell.

The video analysis aimed to define the density and size of the studied species, as well as the habitat they colonized. A 2 × 2 m grid was created and overlaid on the video tracks. Within each 2 × 2 m cell, a snapshot covering 1 m² surface was extracted from the video footage and

Table 1

Features of the surveyed sites. Information covers the area to which the sites belong, the site identification code (ID, which correspond to the different ROV/SSDs video transects), coordinates of the mid-point indicated as degree and decimal minutes (EPSG:4326 - WGS 84), site depth range, its total length, and the method by which the HD videos were collected.

Area	Site ID	Latitude	Longitude	Depth (min - max, m)	Length (m)	Survey method
Costacuti (CC)	CC_01	41° 21.92647' N	12° 37.05593' E	37–41	583	ROV
	CC_02	41° 22.04159' N	12° 36.99647' E	35–40	480	
	CC_03	41° 22.05853' N	12° 36.68500' E	33–41	413	
	CC_04	41° 22.14710' N	12° 36.60164' E	35–42	792	
Capo Linaro (CL)	CL_01	42° 0.98941' N	11° 51.09061' E	32–39	523	ROV
	CL_02	42° 0.98128' N	11° 50.95358' E	27–39	546	
	CL_03	42° 0.99237' N	11° 50.63908' E	22–27	954	
	CL_04	42° 0.82485' N	11° 50.13564' E	22–43	486	
	CL_05	42° 0.95773' N	11° 49.96738' E	21–34	482	
	CL_06	42° 1.01600' N	11° 49.69511' E	22–28	381	
Isola del Giglio (GL)	GL_01	42° 19.01401' N	10° 55.08524' E	10–48	230	SSD
	GL_02	42° 19.72963' N	10° 53.96895' E	10–45	339	
	GL_03	42° 22.40027' N	10° 52.73871' E	11–43	240	
	GL_04	42° 20.24941' N	10° 53.37407' E	10–48	327	
	GL_05	42° 23.05143' N	10° 52.65884' E	08–43	360	
	GL_06	42° 23.33011' N	10° 52.78119' E	10–49	358	

examined to measure species occurrence, density *per* species (number of colonies m^{-2}), maximum colony size, and habitat type. The representative area of $1 m^2$ was estimated using laser pointers as scale, while the correspondence between the measured area and the $2 \times 2 m$ cell was determined by matching times of the video and USBL positioning system. Snapshots extracted from the video were analyzed using *ImageJ* software to gain the aforementioned data. Colony size was exclusively assessed for those colonies that were not perpendicular to the camera lens plane, and reported as size class. Three colony size classes [small (S), medium (M), and large (L)] have been defined for each species (Table S1), based on ranges available from the literature and following the approach defined by Enrichetti et al. (2019a) and Gatti et al. (2015). The maximum size class found in the $1 m^2$ analyzed snapshot was then used to characterize the corresponding $2 \times 2 m$ cell. Habitat types were defined following the recently updated Barcelona Convention classification of marine benthic habitats (Montefalcone et al., 2021). Six habitat types hosting the studied species have been defined and mapped along the transects: association with photophilic algae (Pho), association with *Cystoseira/Ericaria* spp. (Cys), emisciaphilic red algal mats dominated by *P. crista* and *Osmundaria volubilis* (Linnaeus) R.E. Norris 1991 (Phy), coralligenous reefs (Cor), rhodoliths and association with *Peyssonnelia* spp. developing on detritic bottoms (Pey), facies with sponges in overhangs (Spo). The described habitats are shown in Fig. S1. Then, the information gained by video analysis was inserted in the corresponding $2 \times 2 m$ cell of the grid by using Quantum GIS software (QGIS).

2.2.3. Oceanographic variables

Oceanographic variables were downloaded from the Copernicus Marine Environment Monitoring Service (CMEMS; Escudier et al., 2020; Teruzzi et al., 2021) and used as predictors of species densities. The multilevel raster data have a spatial resolution of $1/24^\circ$ (ca 5 km) and 16 vertical levels up to 50 m of depth with mean intervals of $3.11 \pm 0.93 m$. Despite being significantly different from the resolution of terrain and biological variables, these Copernicus products provide the most suitable option for characterizing oceanographic features at the bottom level. The raster data (Copernicus products: MEDSEA_MULTIYEAR_PHY_006_004 and MEDSEA_MULTIYEAR_BGC_006_008) includes reanalyzed integrating models and *in situ* observations to create a continuous reconstruction of the historical physical and biogeochemical features across the entire Mediterranean basin (Cossarini et al., 2021). We considered the following variables (11) during a 10-year interval (from 01/01/2008 to 31/12/2018, Table S1): temperature (T), salinity (S), both eastward (Es) and northward (Ns) current speed, chlorophyll *a* mass concentration (CHL), phytoplankton concentration (PHYC), net primary production (NPPV), dissolved molecular oxygen (DOX), nitrate (NIT), ammonium (NH4) and phosphate (PHO) concentration. The 10-year period aligns with roughly half the duration of the life cycle of the species with the shortest lifespan among those analyzed (see “Description of the study species” in the Supplementary materials). After downloading the raster, we extracted variable values for the pixels intersecting with the 16 transects. The values were then averaged over the entire study period to characterize the physico-chemical features of the water masses occurring in the study sites. Values were extracted from the depth interval corresponding to the mean depth of each $2 \times 2 m$ cell characterized by the presence of the studied species, and assigned to each cell.

2.3. Statistical analysis

The non-parametric Kruskal-Wallis test was used to assess the differences in the colonies' density for each of the three species among the following factors: study areas, colony size, habitat type, and depth. The latter variable was categorized in 4 depth ranges: 10.0–20.0 m; 20.1–30.0 m; 30.1–40.0 m; 40.1–50.0 m. If significant differences occurred according to the Kruskal-Wallis test, a pairwise multiple comparison was performed by the Dunn's test with a Bonferroni

correction. Kruskal-Wallis and Dunn's tests were performed using the “dunnTest” function in R package *FSA* version 0.9.5 (Ogle and Ogle, 2017).

Oceanographic variables were standardized to facilitate comparison of effect sizes, and their correlation was calculated (Fig. S2). To avoid multicollinearity between some variables, we removed from further analysis NPPV and CHL because they exhibited a high correlation with NH4 and PHYC. These variables were retained because they provide information of concentration of ammonium, which can be compared with nitrate and phosphate nutrients, and phytoplankton abundance, rather than primary productivity. The other variables were retained during model estimation to help the ecological interpretation.

To explore the influence of terrain and oceanographic variables on the variability of gorgonian distribution and density distance-based linear modeling (DistLM) was performed using Primer v-5.0. Habitat type, terrain, and oceanographic variables were normalized through a stepwise procedure that tested their importance. Marginal tests were also performed to assess the significance of each variable separately. Prior to DistLM, the categorical variable “habitat type” was transformed into six binary variables (as many as the nominal categories) and then grouped and treated as a single predictor variable by the DistLM analysis. Dissimilarity matrices were produced using Euclidian distance for the habitat type, terrain, and oceanographic variables, while Bray Curtis similarity was used for the species density, after root-squared transformation of density data. Distance-based redundancy analysis (dbRDA) was then applied using Primer v-5.0 to visualize the effect, strength, and direction of the different variables in the ordination plots per areas and species.

A Generalized additive model (GAM) was used to test the non-linear response of the total density of colonies per cell (*i.e.*, sum of density of colonies belonging to the three species, used as a proxy for the formation of coastal MAFs) respect to terrain, oceanographic and biological covariates. To consider other potential spatial effects produced by unmeasured parameters, latitude and longitude were smoothed as interaction terms weighted by study area and a limit on the degree of freedom ($k = 40$) was set to avoid overfitting (Wood, 2006). Since the response variable was a count data (density of colonies), it was analyzed using a GAM model with negative binomial likelihood and natural logarithm as link function. The GAM was estimated using the “gam” function of the R package *mgcv* version 1.8–42 (Wood and Wood, 2015).

The Akaike's information criterion (AIC; Burnham and Anderson, 2002) was used as model selection criteria for both DistLM and GAM. In all the analyses, a level of significance of 0.05 (p -value < 0.05) was selected.

3. Results

3.1. Abundance and spatial distribution of the gorgonian species

The analysis of video transects revealed a total of 1960 cells with species occurrence: the three studied species were present in all the study areas, with marked differences in their distribution and abundance among areas and sites. The three species were found together at 10 out of the 16 sites studied (Table 2). In contrast, 4 sites had two species present, while two sites, both located on the top of the Costacuti bank, exclusively hosted one species (*E. singularis*). Overall, *E. cavolini* was the most frequent species representing 43.4% of total observations (850 cells with species occurrence) and reaching the highest maximum density recorded ($38 colonies m^{-2}$). *Paramuricea clavata* accounted for 30.4% of observations (594 cells) and maximum densities of $35 colonies m^{-2}$. *Eunicella singularis* showed both frequency and density lowest values, 26.0% of observations (516 cells) and $23 colonies m^{-2}$ respectively (Table 2). Overall, *E. cavolini*, *E. singularis*, and *P. clavata* spanned all over the investigated bathymetrical range: 10–48 m, 16–45 m, and 22–47 m of depth, respectively. Density of colonies significantly differed (Kruskal-Wallis test, p -values < 0.05) among depth ranges for all the

Table 2

Species presence, density of colonies, and bathymetric distribution of the three studied species. Mean and maximum density (expressed as the number of colonies m^{-2}), occurrence (number of cells characterized by species presence), percentage of cell per size class minimum and maximum depth range are given per site.

Species	Area	Site ID	Mean density \pm SD (colonies/ m^2)	Max density	Number of observation	Size classes (%)			Bathymetric distribution range (m)	
						S	M	L		
<i>Eunicella cavolini</i>	Costacuti (CC)	CC_01	3.0 \pm 3.4	12	10	30	70	0	42–44	
		CC_02	–							
		CC_03	6.5 \pm 5.0	18	20	35	60	5	33–40	
		CC_04	–							
		Capo Linaro (CL)	CL_01	–						
			CL_02	1.8 \pm 1.1	3	5	40	60	0	31–38
	CL_03		3.2 \pm 2.2	8	48	40	50	10	21–27	
	CL_04		6.5 \pm 4.4	15	22	50	50	0	22–24	
	CL_05		9.1 \pm 4.7	24	100	49	46	5	21–25	
	CL_06		2.8 \pm 1.5	18	13	31	46	23	24–28	
	Isola del Giglio (GL)	GL_01	14.4 \pm 9.5	35	72	7	47	46	22–48	
		GL_02	10.2 \pm 7.8	25	28	11	89	0	17–25	
		GL_03	15.9 \pm 9.4	18	182	9	77	14	10–47	
		GL_04	6.5 \pm 6.3	25	81	9	84	7	19–44	
		GL_05	16.6 \pm 7.3	30	123	0	95	5	15–43	
		GL_06	14.2 \pm 8.6	35	146	3	82	16	10–46	
	<i>Eunicella singularis</i>	Costacuti (CC)	CC_01	1.5 \pm 0.7	2	2	100	0	0	43–44
			CC_02	3.9 \pm 2.7	12	97	11	30	59	35–41
CC_03			1.0 \pm 0.2	1	1	100	0	0	37–38	
CC_04			15.0 \pm 2.8	10	94	9	47	45	35–38	
Capo Linaro (CL)		CL_01	2.0 \pm 0.2	2	1	0	100	0	37–38	
		CL_02	1.6 \pm 0.9	3	5	40	20	40	27–36	
		CL_03	1.7 \pm 1.0	4	11	18	82	0	21–26	
		CL_04	1.4 \pm 0.7	3	12	8	92	0	28–42	
		CL_05	1.2 \pm 0.6	3	14	43	43	14	21–34	
		CL_06	3.0 \pm 0.1	3	1	100	0	0	26–27	
Isola del Giglio (GL)		GL_01	–							
		GL_02	1.4 \pm 0.6	3	30	0	10	90	20–37	
		GL_03	2.8 \pm 1.8	8	44	5	5	91	20–39	
		GL_04	2.6 \pm 1.5	5	30	93	7	0	27–33	
		GL_05	1.6 \pm 0.7	3	29	3	14	83	22–38	
		GL_06	8.8 \pm 5.3	23	170	1	4	95	16–45	
<i>Paramuricea clavata</i>		Costacuti (CC)	CC_01	9.5 \pm 6.2	27	104	5	33	63	37–44
			CC_02	–						
	CC_03		8.1 \pm 7.0	25	64	27	47	27	33–40	
	Capo Linaro (CL)	CC_04	1.4 \pm 0.5	2	5	80	20	0	38–40	
		CL_01	4.6 \pm 2.9	8	5	0	40	60	37–38	
		CL_02	12.4 \pm 6.5	20	28	7	71	21	29–38	
		CL_03	3.9 \pm 2.4	8	15	0	47	53	22–28	
		CL_04	6.7 \pm 6.4	30	94	11	44	46	22–41	
		CL_05	1.6 \pm 1.1	5	15	47	47	7	25–25	
	Isola del Giglio (GL)	CL_06	2.7 \pm 1.6	5	12	8	50	42	24–28	
		GL_01	8.6 \pm 5.3	22	40	3	38	60	23–45	
		GL_02	–							
		GL_03	16.1 \pm 10.6	32	32	0	31	69	28–47	
		GL_04	–							
		GL_05	14.0 \pm 8.5	30	49	2	8	90	27–43	
	GL_06	16.1 \pm 10.6	35	131	4	35	61	25–48		

three species (Fig. 3a). The density of *E. singularis* decreased with increasing depth, while the density of *P. clavata* showed the opposite pattern. In contrast, *E. cavolini* did not exhibit a clear relationship with depth, though its mean density was higher at depths above 20 m.

Giglio Island was notable for hosting the highest number of observations, as well as the highest mean and maximum density values for all three species (Table 2). The density of colonies showed a decreasing trend from Giglio Island to Costacuti and Capolaro (Fig. 3b): the Kruskal-Wallis test revealed significant differences in the density of colonies of the three species among areas (Kruskal-Wallis test, p-values < 0.05). Specifically, the multiple pairwise comparisons highlighted that gorgonian populations hosted at Giglio Island were significantly denser if compared to the other areas, except when *E. singularis* was compared with Costacuti bank. On the other hand, there was no significant difference in *E. cavolini* density of colonies between Capo Linaro and Costacuti. All the species showed a patchy distribution at the site level. This was demonstrated by the large SDs reported in Table 2 and the wide range of values included in the interquartile range of the boxplots characterizing Giglio Islands in Fig. 3b, indicating a large dispersion of

density values. Table S2 reports the detailed output of multiple pairwise comparisons (Dunn's tests).

A relation between colony size class and density of colonies was evident for all three species (Kruskal-Wallis test p-value < 0.05 ; Fig. 3c). The areas with higher densities were characterized by the presence of large-sized colonies, while lower abundances were usually associated with the occurrence of sparse small colonies. This pattern was not significant when comparing M and S colonies of the species *E. singularis* exclusively.

Fig. 3d illustrates the habitat preferences of the three gorgonians: their occurrence and density significantly varied according to the habitat type. *Eunicella cavolini* was found in 3 out of the 6 habitat types characterizing the study areas, with the majority (93.0%) of the observations occurring in association with coralligenous reefs (Cor), and secondarily in facies with sponges in overhangs (Spo = 4.7%) and emisciaphilic red algal mats (Phy = 2.3%). The denser aggregations were found on coralligenous reefs; the multiple pairwise comparisons revealed that density of colonies significantly decreased in red algal mats while no significant differences occurred between coralligenous

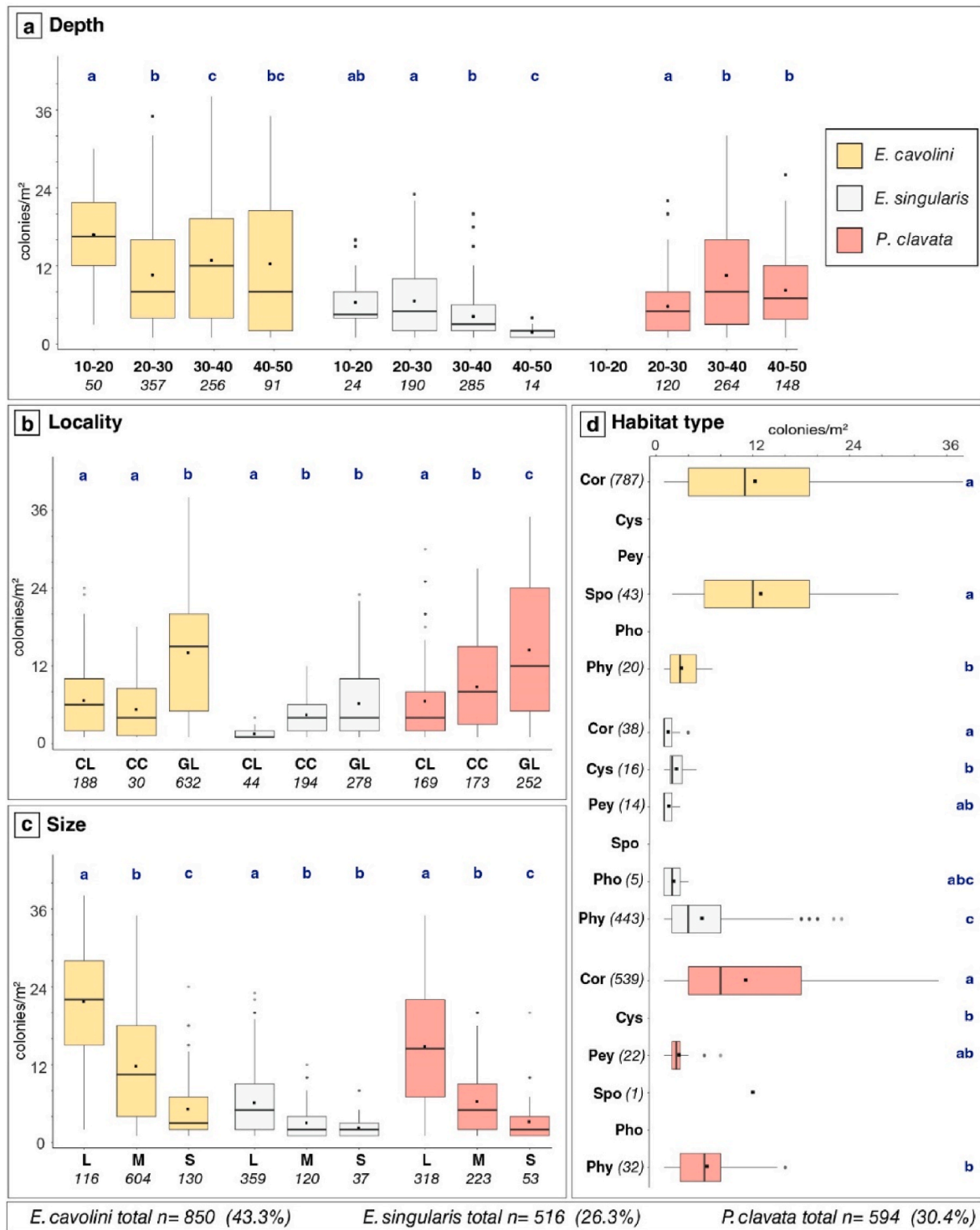


Fig. 3. Plots showing the density of colonies belonging the studied species among depth ranges (a), in the study areas (b), for different size classes (c), and in habitat types (d). The y axes in (a), (b), and (c) and the x axis in (d) represent the n° of colonies/m² plotted against the abovementioned variables. The letters above the boxplots indicate the results of pairwise multiple comparisons through Dunn's test among the levels of the factor area, size, and habitat type. Area: CL - Capo Linaro promontory, CC - Costacuti bank, GL - Giglio Island. Colony size classes: S - small, M - medium, L - large. Habitat type: Cor - coralligenous reefs, Cys - association with *Cystoseira/Ericaria* spp., Det - coastal detritic bottoms, Ove - overhangs, Pho - association with photophilic algae, Phy - emisciaphilic red algal mats.

reefs and facies with sponges in overhangs (Table S2). *Eunicella singularis* was distributed over a wide range of different habitats and its density of colonies significantly varied among habitat types (Table S2). A marked preference was given for emisciaphilic red algal mats (85.8% of the observations), where the highest mean and maximum density were reported. Few observations (14.2% of the total), characterized by low

density values (less than 5 colonies m⁻²) occurred on coralligenous reefs (7.5%), *Cystoseira/Ericaria* spp. beds (Cys = 3.1%), rhodoliths and association with *Peyssonnelia* spp. on detritic bottoms (Pey = 2.7%), and photophilic algae bottoms (Pho = 0.9%). *Paramuricea clavata* mostly occurred with high densities of colonies on coralligenous reefs (90.7% of the observations), and secondarily on emisciaphilic red algal mats

(5.2%) and rhodoliths and association with *Peyssonnelia* spp. on detritic bottoms (3.7%). A single observation was attributed to facies with sponges in overhangs. The denser aggregations were restricted to coralligenous reefs and emisciaphilic red algal mats, although the former habitat significantly supported higher density levels (Table S2).

3.2. Relationships with terrain and oceanographic variables

The linear model selected by DistLM explained 63.8% of the total variance of gorgonian densities and identified both terrain, oceanographic, and biological parameters as variables that significantly contributed to the observed patterns, as indicated by the statistical significance obtained in the marginal and sequential tests (p -value < 0.05 , Table S3). The habitat type contributed to the highest percentage of variance explained (42.4%), followed by ammonium (NH4) and phytoplankton concentration (PHYC) explaining 6.6% and 6.3, respectively. While bottom current speed (Es), seafloor ruggedness (VRM), and depth contributed for 2.7, 1.6, and 1.5% respectively, all the other variables explained $< 1\%$ of variance (Table S3).

The dbRDA plot from DistLM (Fig. 4) indicated quite striking differences among the study areas, as well as a clear spatial separation of *E. singularis* with respect to the two other species. Variables related to the

habitat type (mostly Cor and Phy), nutrients (PHO and NIT), and phytoplankton concentrations (PHYC), along with terrain parameters (VRM and Slope), mainly structured the samples along the first axis, while temperature (T), depth, dissolved oxygen (DOX), and ammonium concentration (NH4) showed a correlation with the second axis. This clearly divided *E. singularis*, mostly occurring on emisciaphilic red algal mats and shallower depths, from *E. cavolini* and *P. clavata*. These two species displayed a strong affinity with coralligenous reefs and factors related to the seafloor morphological complexity, such as slope and rugosity (VRM), as well as to nutrient concentration. Additionally, a positive relationship between *P. clavata* and depth was noticeable.

3.3. Factors driving coastal MAFs formation

The total density of colonies (reported as the number of colonies m^{-2} per cell) was here used as a proxy indicating the formation of complex coastal MAFs by the three gorgonian species (Table S4). The portion of deviance explained by the model as well as the pseudo- R^2 were 61.5% and 0.60, respectively. Depth, slope, and seafloor ruggedness were considered as terrain covariates, whereas habitat types and the number of species found per cell were the biological covariates included in the model formula. However, the selection of the best model (lower AIC and

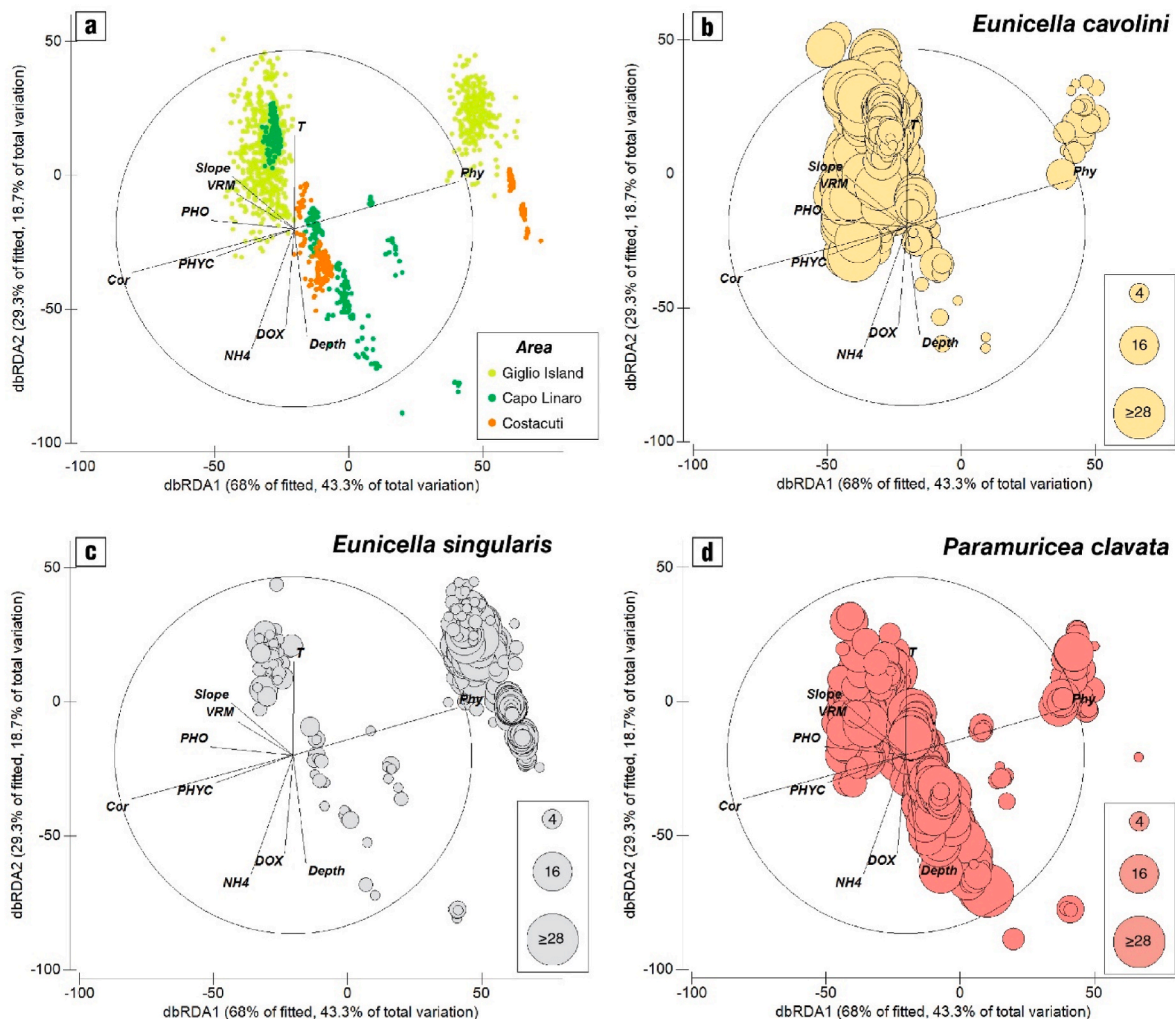


Fig. 4. Distance-based redundancy analysis (dbRDA) plots showing ordination of the DistLM model and the relative influence of the fitted predictor variables, indicated by the vectors. Note that only variables having a Pearson correlation coefficient > 0.3 are shown. In (a) samples are labeled according to the study area, while the other plots (b to d) illustrate the abundances of each species in the two-dimensional space determined by dbRDA. Circle size is proportional to the number of colonies m^{-2} . T-temperature; VRM-Vector Ruggedness Measure; PHYC-phytoplankton concentration; DOX-dissolved molecular oxygen; NH4-ammonium concentration; PHO-phosphate concentration; Cor-coralligenous reefs; Phy-emisciaphilic red algal mats.

portion of explained deviance) did not take into account the contribution of oceanographic covariates.

A linear positive relationship emerged between the density of colonies and number of species responsible for coastal MAFs formation: multispecific MAFs were characterized by a higher number of colonies m^{-2} and, therefore, provided more structured and complex habitats (Fig. 5a). The density of colonies decreased significantly in all the habitat types if compared to coralligenous reefs, which represents the condition defining the intercept. Only density in overhangs (Ove) did not return statistical significance. The dependent variable decreased almost linearly with depth; conversely, it exhibited exponential and asymptotic increasing trends regarding seafloor morphological complexity, in other words the higher slope and VRM the higher density of colonies (Fig. 5b). Smoothing effects of longitude and latitude on the gorgonian density showed different patterns according to the area (Fig. 5c). The steepness of the smoothing gradient suggested a strong positive effect on the dependent variable along NW-SE direction at Capo Linaro, and NE-SW gradient at both Costacuti and Giglio Island. Such patterns highlight the upstream portion of each area directly impinged by the northwestward general cyclonic Tyrrhenian circulation. At Giglio island the smoothing function showed higher change along the longitude axis (X).

4. Discussion

The present work investigated at a fine scale (resolution in the order of 2×2 m) the density and spatial distribution patterns of three gorgonian species between 8 and 49 m depth in a poorly investigated sector of the Tyrrhenian Sea. The outcomes highlighted the pivotal role of terrain, oceanographic, and biological parameters in driving both species distribution and MAFs formation in coastal habitats, as shown in the following sections.

4.1. Spatial distribution patterns of the species

Mediterranean coastal shallow habitats support less diversified gorgonian assemblages when compared to those thriving at greater depths (Bo et al., 2012; Grinyó et al., 2016). *Eunicella cavolini*, *E. singularis*, and *P. clavata* were observed in all the studied areas dwelling on rocky or detritic seabeds between 10 and 50 m depth. The gorgonian assemblages were predominantly monospecific (81% of the observations), with two and three species co-occurring in 18% and 1% of the cells, respectively. *Eunicella cavolini* was the most abundant species, both in terms of occurrence and density values, as opposite to *E. singularis* which was the least abundant species, although it occurred in most of the sites. This pattern contrasts with observations carried out along Spanish and French coasts at comparable depth ranges, where *E. singularis* was reported as the most common and abundant among gorgonian species (Blouet et al., 2022; Gori et al., 2011). On the other hand, *P. clavata* exhibited significant patchiness, similarly to what observed by Gori et al. (2011), with both the number of observations and mean density varying widely between sites and areas.

The mean and maximum density of colonies values align with the range of variability documented in other regions of the Mediterranean Sea through direct SSD sampling (Kipson et al., 2015; Linares et al., 2008; Munari et al., 2013; Sini et al., 2015) and video analysis (Gori et al., 2011). The cited works highlighted the substantial variability in the density of the three species across the Mediterranean regions, which can potentially obscure any differences stemming from the sampling methodology employed (ROVs and SSDs collected videos versus SSDs direct samplings). However, it is essential to emphasize that, despite the utilization of high-resolution images, the lack of a three-dimensional perspective of the habitat could affect the estimation in cases of highly dense MAFs and the ability to detect juvenile colonies. This could lead to underestimation of colonies' density when using video analysis instead of direct sampling. However, the former methodology allowed for

examining extensive portions of the substrate, thereby capturing species' ecological patterns at the investigated sites more effectively, without limiting the observations where MAFs were present.

Significant variations in species occurrence and density were observed among different study areas, as well as within the same study area, where a large variability was also observed among sites, and even within the same sites. The differences between the three areas can be attributed to the distinct environmental settings they represent, such as island, coastal area, and isolated bank, which are subjected to different processes linked to the availability of hard substrates and hydrodynamics. The highest occurrences and densities of colonies were reported at Giglio Island; this could be due to the topographic complexity of the seafloor in western portion of the island, featuring steep and continuous rocky bottoms ranging from 5 to over 70 m of depth, which results in a mosaic of habitat types at small spatial scale with different algal dominance (Casoli et al., 2016). The presence of extensive and complex rocky ridges can interfere with the prevailing currents in the area, creating local hydrodynamic phenomena favorable to colony settlement and growth. These seafloor's features serve as proxies for food supply and have been reported to influence the distribution of Mediterranean octocorals (Blouet et al., 2022; Cocito et al., 1997). Capo Linaro, in contrast, has less continuous rocky substrates available for colonization, with steep walls and sparse outcrops scattered over sedimentary bottoms (Pierdomenico et al., 2021), whereas Costacuti bank rises from the surrounding shelf within a narrow bathymetric range (33–45 m depth) and represent the area with the lowest availability of hard substrates, yet hosting higher densities of gorgonians compared to Capo Linaro. At Costacuti bank, high densities of *E. cavolini* and *P. clavata* were exclusively observed along the southwestern flank exposed to the prevailing northwestern current, while no observations were reported along the more repaired northeastern flank, suggesting a strong role also of the local hydrodynamics in driving species distribution.

Along with the availability of hard substrates, lithology can also influence the variation in gorgonian abundance. However, the observed pattern based on lithological differences between areas (granite at Giglio Island, and limestone at Capo Linaro and Costacuti) was not consistent with that reported by Canessa et al. (2020), who found limestone as a more suitable substrate for settlement of gorgonians such as *E. cavolini*.

The patchy distribution reported within same sites is favored by the settlement near the putative parental colony (Linares et al., 2008) and by the limited dispersal capacity of the larva (Guizien et al., 2020). This may explain the pattern observed in this study for all three species, where higher density of colonies was associated with larger colonies. This result identifies populations characterized by conditions of limited disturbance and indicates areas suitable for stably supporting high densities and biomasses of the species due to hosting older colonies.

Eunicella cavolini, *E. singularis*, and *P. clavata* exhibited different ecological requirements and habitat selection based on terrain, oceanographic, and biological variables. Habitat types mostly contributed to explain the emerging patterns, with coralligenous reefs and emiscia-philic red algae mats hosting most of the observations and dense aggregation of the studied species. The occurrence of *E. cavolini* and *P. clavata* on coralligenous reefs is consistent with several studies carried out on shallow and deep Mediterranean shelf substrates (Enrichetti et al., 2019b; Grinyó et al., 2016; Moccia et al., 2021). On the other hand, the role of emiscia-philic algal mats in hosting dense populations of *E. singularis* and *P. clavata* is reported here for the first time. Sediment and associated organic matter retained by *P. crista* mats (Bianchi et al., 2023) could be resuspended by near bottom hydrodynamics, providing a food source that can support these populations.

Among terrain variables, slope and ruggedness (VRM) influenced *E. cavolini* and *P. clavata* colonization, although the latter was observed on deep horizontal substrates, as well. This result partially contrasts with recent models identifying slope as an important predictor shaping the niche of *P. clavata* (Boavida et al., 2016). Indeed, high sedimentation rates could limit settlement of hard bottom invertebrates (Birrell et al.,

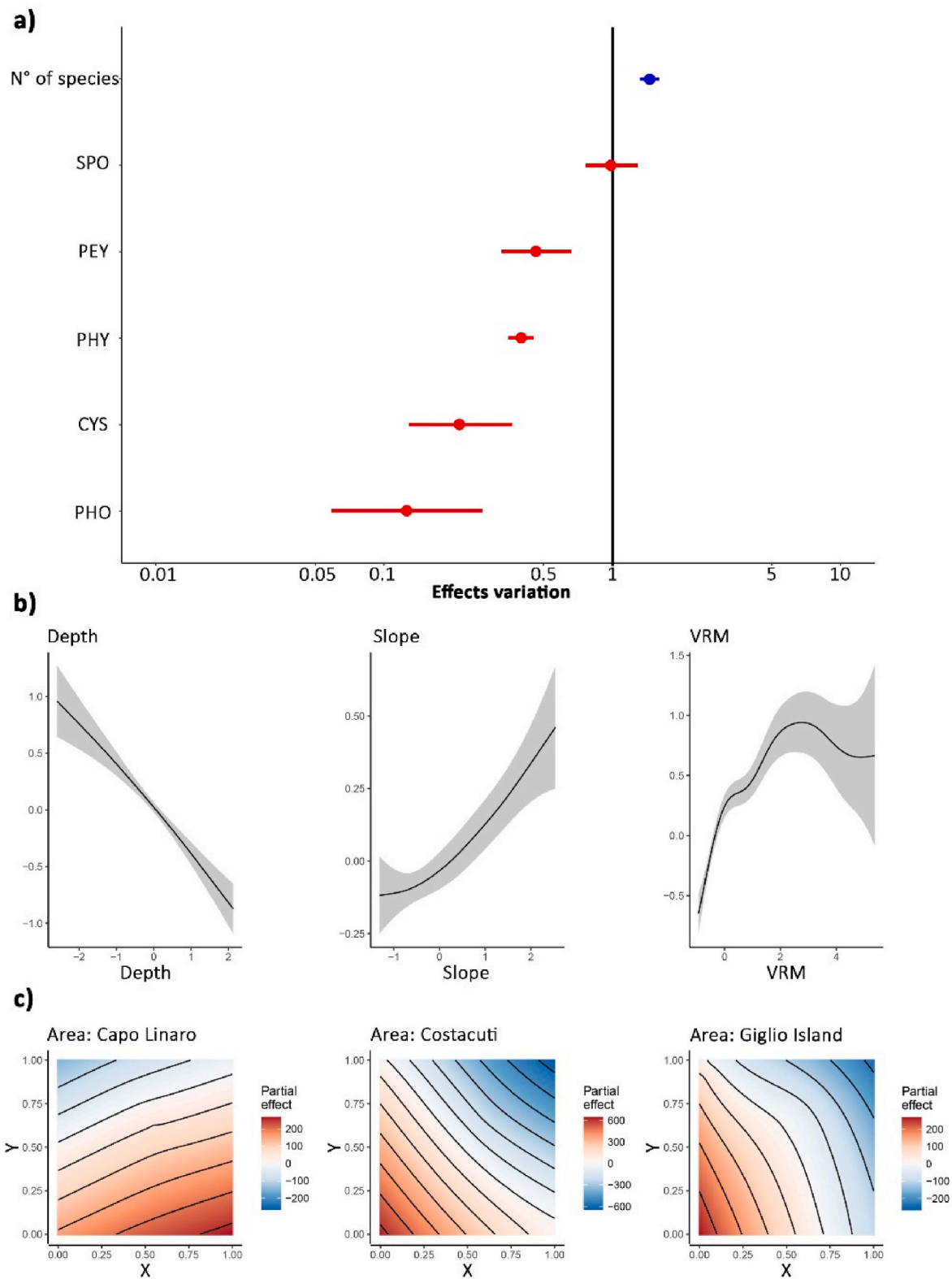


Fig. 5. (a) Estimated effect variation of linear terms in the GAM; blue and red dots indicate positive and negative variations with respect to the corner point. Vertical lines depict the 95% confidence interval: if they meet the intercept axis, the corresponding effect is not statistically significant. (b) Response curves of the total density of colonies to bathymetric variables in the GAM for the smoothed terms depth, slope, and ruggedness (VRM). The black line represents the smoothed function, whereas the gray area indicates the 95% confidence interval. The X-axis reports the scaled values of the covariates. (c) Smoothing terms of longitude (X) and latitude (Y) for the GAM model: smoothing isotherms are arranged according to the gradient defined by the red-blue palette.

2005), while high slope gradients and complex topography (*i.e.* high VRM) interact with water flow increasing horizontal and vertical current speed. Such enhanced hydrodynamics not only inhibit the deposition of fine sediment, but also increase the prey capture rates of passive suspension feeders (Rossi and Rizzo, 2021).

Paramuricea clavata was the only species showing frequent and dense aggregation in deeper areas: the depth range considered here was limited, but it is representative of the distribution of hard bottoms in the study areas. Furthermore, shallow colonies of this species were associated with complex topography and vertical walls, while deeper ones colonized less steep and sparse rocky outcrops, which are widely distributed in the deeper sectors of our study areas. Conversely, *E. singularis* preferentially colonized horizontal and sub-horizontal rocky bottoms with emisciphilic algal communities, mostly above 30 m of depth, where water movement, light exposure, and sediment resuspension can support mixotrophic nutrition (Schmidt et al., 2021). Aspect (*i.e.* seabed orientation) was the sole not significant terrain predictors, as reported in similar studies (Blouet et al., 2022).

Oceanographic variables were acquired at significantly different resolution if compared to the biological and terrain ones: this approach is not reliable in revealing small-scale variations, but allows the characterization of bottom water masses over wide geographical, temporal, and bathymetric ranges. This could lead to an underestimation of the importance of certain parameters, as northern and southern current speeds that marginally contributed to explaining specific patterns. Bottom topography may be considered a more informative proxy for small-scale hydrodynamics than basin circulation which, on the other hand, influences connectivity among populations (Sciascia et al., 2022). Nutrients and phytoplankton concentrations favored *E. cavolini* and *P. clavata* presence and dense aggregations: primary production can be positively linked to the abundance of small zooplankton on which the species mostly feed on. However, resource availability for benthic suspension feeders is mediated through stochastic and pulse events (Ribes et al., 2007; Rossi and Rizzo, 2021) that for their nature are difficult to take into account in detail. As for *E. singularis*, the results are not consistent with the capacity of the species to uptake dissolved nutrients as food sources (Gori et al., 2012).

4.2. Coastal animal forest formation

The MAF definition does not specify a threshold for the number of organisms needed to categorize a given area as a forest (Orejas et al., 2022). In the present study, we used the density of habitat-forming species as a quantitative descriptor of seascape complexity, also based on the finding that large colonies are associated with higher density aggregations.

Coastal MAFs in central-northern Tyrrhenian Sea are mainly hosted on coralligenous reefs: likely, bioconstructions provide structural long-term stability and microhabitat heterogeneity, and develop on steep walls, meeting the ecological requirement of *E. cavolini* and *P. clavata* (Weinbauer and Velimirov, 1995). In photophilic environments, seascape complexity provided by octocorals decreased in favor of forests dominated by algal species more adapted to light exposed conditions, such as *Cystoseira/Ericaria* spp., as observed in Mediterranean coastal areas (Boudouresque et al., 2016). However, the effects of temperature (Garrabou et al., 2022), as well as poor stability and multidirectional hydrodynamic flows in shallow habitats (Teixidó et al., 2013) might contribute to explain the observed pattern, along with biological competition with autotrophs. Furthermore, both the mentioned factors negatively affect the octocoral prey capture rate (Gori et al., 2012; Rossi and Rizzo, 2021). In this regard, the emisciphilic red algal mats deserve further attention as they can host, together with already well known habitat (*i.e.*, coralligenous reefs and detritic bottoms), dense gorgonian aggregations highlighting their role in ecological processes supporting coastal biodiversity (El-Khaled et al., 2022). In this habitat, the resuspension of sediment trapped by the red algal mats could provide an

important food source, particularly for species (*i.e.*, *P. clavata*) that rely on particulate and sedimentary organic matter in their diet (Cocito et al., 2013). Multispecific gorgonian assemblages increased the complexity of the seascape. However, most observations showed a single species per cell, resulting in significantly lower diversity compared to deeper Mediterranean shelf environments (Grinyó et al., 2016). This pattern reflected differences in the analysis of species' ecological requirements and could also be explained in the light of reducing competition for space among the studied species in the shallow coastal waters.

Terrain variables were highly correlated with the total density of colonies. Due to the absence of extensive hard bottoms suitable for colonization and the presence of large sediment-covered areas, complex MAFs decreased with depth. On the contrary, slope and ruggedness positively contributed to the complexity of MAFs: such features significantly influence octocoral distribution at coarse and fine spatial scale in both temperate and tropical habitats (Martínez-Quintana et al., 2023; Miyamoto et al., 2017). This suggests that morphological complexity of coastal bottoms supports a high density of gorgonian by creating areas that interact with the local hydrological regime, and presumably increase the hydrodynamics of the benthic boundary layer. This structural heterogeneity, combined with the hydrodynamic patterns, is responsible for the spatial gradients in octocoral density of colonies within each study area. In fact, the smoothing gradients drawn by using GAM identified the southern portions of all the three areas in hosting dense gorgonian aggregations. These southern portions are more affected by the unidirectional northward flowing currents of Tyrrhenian surface waters (Pinardi and Masetti, 2000). Although in the GAM model the oceanographic parameters did not contribute to increase the model fit, such result highlights the strong influence of large-scale currents' path in favoring the development of complex MAFs at specific locations of the study areas.

4.3. Potential applications to conservation management

The integration of biological observations from seafloor HD images, terrain and oceanographic parameters extracted from remote sensing technology presented in this study enhances our understanding of the ecological requirements of the three habitat providers in the coastal areas. Gaining insights into the factors that influence the formation of MAFs is essential for initiating efforts to conserve these endangered habitats. Despite the pivotal role of the three species studied here in the functioning of benthic ecosystems and their vulnerability to both climate change and anthropogenic disturbances (Gómez-Gras et al., 2021a), they are not directly included in national or basin regulations enhancing their protection and conservation. The emerging patterns presented in this work can support conservation strategies at the site level, by identifying small-scale seafloor features prone to host complex MAFs, further implementing the priority areas recently highlighted along the Italian coasts (Liconti et al., 2022). This is especially urgent in light of the projected local extinction that these species will face in the near future (Zentner et al., 2023), particularly in the shallow zones where Tyrrhenian MAFs thrive. The outcomes of this study can be further developed to create cartographic products of habitat suitability, which would facilitate ecological restoration interventions by transplanting colonies found as by-catch (Casoli et al., 2021). These products will highlight areas suitable for transplantation based on the ecological requirements of the species or able to support MAFs, and integrate baseline data of species past presence.

CRedit authorship contribution statement

Martina Pierdomenico: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Filippo Pandolfi:** Investigation, Formal analysis. **Gianluca Mancini:** Writing – review & editing, Investigation, Formal analysis. **Daniele Ventura:** Writing – review & editing,

Investigation, Formal analysis. **Matteo Falco**: Writing – review & editing, Investigation, Formal analysis, Conceptualization. **Andrea Belluscio**: Writing – review & editing, Conceptualization. **Giandomenico Ardzzone**: Writing – review & editing. **Giovanna Jona-Lasinio**: Writing – review & editing, Methodology, Formal analysis. **Edoardo Casoli**: Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The work is all original research carried out by the authors. All authors agree with the contents of the manuscript and its submission to the journal. No part of the research has been published or under consideration elsewhere, while it is being considered for publication in this journal. The present research does not relate to any other manuscript of a similar nature that the authors have published, in press, submitted or will soon submit to *Marine Environmental Research* or elsewhere.

The authors declare that they have no conflict of interest. Founding are acknowledged in the manuscript in the specific section.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2024.106663>.

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