

Article

Shedding Light on the Italian Mesophotic Spongofauna

Margherita Toma ^{1,2,*}, Marzia Bo ^{2,3,4}, Marco Bertolino ^{2,3,4}, Martina Canessa ², Michela Angiolillo ^{1,5}, Alessandro Cau ⁶, Franco Andaloro ⁵, Simonepietro Canese ⁵, Silvestro Greco ⁵ and Giorgio Bavestrello ^{2,3,4}

¹ Istituto Superiore per la Protezione e Ricerca Ambientale (ISPRA), 00144 Roma, Italy; michela.angiolillo@isprambiente.it

² Dipartimento di Scienze della Terra dell'Ambiente e della Vita (DISTAV), Università degli Studi di Genova, 16132 Genova, Italy; marzia.bo@unige.it (M.B.); marco.bertolino@unige.it (M.B.); marti.canessa@gmail.com (M.C.); giorgio.bavestrello@unige.it (G.B.)

³ National Biodiversity Future Centre (NBFC), Piazza Marina 61, 90133 Palermo, Italy

⁴ Consorzio Nazionale Interuniversitario per le Scienze del Mare, 00196 Roma, Italy

⁵ Stazione Zoologica Anton Dohrn, 80122 Napoli, Italy; franco.andaloro@szn.it (F.A.); simonepietro.canese@szn.it (S.C.); silvestro.greco@szn.it (S.G.)

⁶ Dipartimento di Scienze della Vita e dell'Ambiente, Università di Cagliari, 09124 Cagliari, Italy; alessandrocau@unica.it

* Correspondence: margherita.toma@isprambiente.it

Abstract: An analysis of 483 remotely operated vehicle (ROV) dives carried out along the Italian coast on hard substrata at mesophotic depths (40–200 m) allowed an overview of the rich sponge diversity (53 taxa) of the deep continental platform to be obtained for the first time. About 40% of the potential actual species diversity was recognisable using ROV, suggesting that this group is among the richest yet underestimated using this technology in contrast to other megabenthic taxa. Additionally, the study allowed us to gather data on the current basin-scale distribution and bathymetric limits of five common and easily identifiable demosponges with up to 55% occurrence in the explored sites: *Aplysina cavernicola*, the group *Axinella damicornis/verrucosa*, *Chondrosia reniformis*, *Foraminospongia* spp., and *Hexadella racovitzae*. Four of these latitudinal distributions were characterised by high occurrence in the Ligurian Sea and a progressive decrease towards the south Tyrrhenian Sea, with an occasional second minor peak of occurrence in the Sicily Channel. In contrast, *Foraminospongia* spp. showed a maximum occurrence on the offshore reliefs and a second one in the North-central Tyrrhenian Sea, while it was almost absent in the Ligurian Sea. Trophic and biogeographic reasons were discussed as possible causes of the double-peak distributions. The vertical distributions support a more consistent occurrence of all considered taxa in deeper waters than previously known. This suggests that they may more typically belong to the mesophotic realm than the shallow waters, owing to a more extensive sampling effort in the deeper depth range. The five target taxa are typical or associated species of seven reference habitats in the recently revised UNEP/SPA-RAC classification. However, they may create such dense aggregations that they should be listed as new facies in the abovementioned classification.

Keywords: demosponges; large-scale distribution; zonation; ROV; reference habitats



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1. Introduction

With more than 720 described species, sponges are one of the benthic groups with the highest species richness in the Mediterranean Sea [1,2]. They play a pivotal role in the functioning of marine benthic ecosystems as recyclers of dissolved and particulate organic matter, reservoirs and sinks of silica, and, for the larger species, ‘key bioengineers’ because of their three-dimensional structures and long lifespans [3–11]. The sponge-dominated habitats can attract fish and invertebrates, also of commercial interest, by increasing the number and complexity of available microhabitats, providing refuge from predators, and serving as spawning and nursery grounds [7,12–14]. Given their diversity and abundance,

they dominate facies and are listed as typical or associated species of numerous reference habitats in the recently revised UNEP/SPA-RAC classification, from the littoral zone to abyssal depths [15].

Although Mediterranean sponge fauna is among the world's most studied, information about deep-sea species remains scarce, especially compared to those found in shallow waters [7,10,16,17]. Data on massive deep-sea sponges mainly derive from dredging or trawling (including individuals collected as bycatch and scientific hauls) [18–20]. Many recent studies have relied on these techniques, benefiting from the possibility of identifying the samples through morphological and molecular analyses, but, on the other hand, the lack of observation of the specimens in situ leaves profound gaps in the knowledge of their ecology [17,21–23]. In the last twenty years, new technologies such as submersibles, autonomous underwater vehicles (AUVs) and remotely operated vehicles (ROVs) that can also collect samples have made the visual exploration of deep-sea environments feasible, significantly increasing knowledge about the composition and vulnerability of the megabenthic communities thriving at mesophotic and bathyal depths, especially in rocky habitats [24–33]. This has provided much data on megabenthic species, including sponges, in their natural habitats [10,16,34–36]. At first, most of the studies targeting the spongofauna focused on peculiar species in limited geographic extension and bathymetric gradients [37–39]. Large-scale datasets covering regions or entire basins in a wide depth range remain scant [40,41].

Various studies have focused on mesophotic (40–200 m) assemblages dominated by massive sponges in the Mediterranean Sea. In the eastern basin, multi-specific sponge aggregations were recently characterised along the Israeli coast by Idan et al. [42], while in the western sector, Santín et al. [10,43] and Dominguez-Carrió et al. [44] described complex sponge assemblages on the continental shelf of the Menorca Channel and in a submarine canyon off Cap de Creus, respectively. More recently, Díaz et al. [17] identified rich sponge assemblages on the sedimentary and rocky bottoms of three seamounts of the Mallorca Channel. Enrichetti et al. [40,45] reported two communities along the Italian coast dominated by sponges (*Axinella* spp. and *Haliclona* cf. *mediterranea*) and extensive sponge grounds dominated by massive keratose sponges in the Ligurian Sea between 40 and 70 m. Other mesophotic assemblages with numerous and abundant sponge species were found in the Amendolara Bank between 120 and 180 m [7] and in the Gulf of St Eufemia (south Tyrrhenian Sea) between 90 and 130 m [46].

Compared to other phyla, identifying Porifera through images is challenging, and sampling is not always easy because of the small size of most species and their encrusting or cryptic habitus [47]. For these reasons, sponges are often cited as common components of deep benthic communities, but their identification remains uncertain, so their diversity and abundance are largely underestimated [16,47,48].

In this study, an extensive dataset obtained from explorative ROV campaigns between 2006 and 2021 at the basin scale (Ligurian Sea, Tyrrhenian Sea, and Sicily Channel) was analysed to define, for the first time, the large-scale distribution of the spongofauna present along the Italian coasts at mesophotic depths. In particular, the large-scale occurrence of the most common and identifiable sponges was obtained and discussed in terms of latitude and depth.

2. Materials and Methods

2.1. ROV Dataset

The dataset included 483 ROV dives, each corresponding to a distinct geographical site. Sites were then grouped into four coastal macro-areas (LIG, Ligurian Sea; NCT, North-central Tyrrhenian Sea; ST, South Tyrrhenian Sea; SC, Sicily Channel) and one offshore macro-area. The latter macro-area included the mesophotic tops of three seamounts: the Santa Lucia Seamount in the Ligurian basin, the Vercelli Seamount in the central Tyrrhenian Sea, and the Palinuro Seamount in the southern Tyrrhenian Sea (offshore reliefs, OR), in the depth range of 40–200 m (Figure S1). About 486 h of video footage and 25,500 photos

taken by high-resolution cameras were analysed, covering ~570,000 m² (hard ground and the surrounding soft bottoms).

2.2. Sponge Diversity

In each site, the presence of large sponges (>3 cm), identified to the lowest possible level, was noted. Taxa (species or genera) were determined based on external morphological features using field guides and the available specialist scientific literature and, when possible, through laboratory analyses of collected samples. The currently valid scientific species names were checked on the World Porifera Database (WPD) [2]. Only those reliably identifiable from the images were considered in the analyses. To estimate the actual diversity of the sponge fauna, the gaps between the considerable species richness based on images (ROV sponge diversity), and the potential true diversity of large sponges, all the taxa, including those identifiable at the species level and those recognisable only as morphotypes, labelled with a sequential number, were counted in 10 random sites.

2.3. Large-Scale Distribution

The percentage frequency of occurrence of each identified taxon was calculated considering the entire dataset and the single macro-areas, and the semi-quantitative abundance of each taxon was defined according to the frequency of observation (on a 0–3 scale: never observed, 0; rare (<3 observations), 1; common (3–10 observations), 2; abundant (>10 observations), 3). The normalised average ROV sponge diversity $\pm$ SE in each considered macro-area was obtained as the average number of taxa identified in each dive in the macro-area.

Multivariate analyses of the sponge diversity matrix were performed using semi-quantitative abundance (1, rare; 2, common; 3, abundant). The offshore relief records were not included in the formal analysis due to their scarcity. The non-metric Multi-Dimensional Scaling (nMDS) plot was produced to ascertain macro-area clustering patterns in the upper (40–100 m) and lower (100–200 m) mesophotic zone. Putative differences were tested using PERMutational ANalysis Of VAriance (PERMANOVA) (factor ‘macro-area’, fixed, 4 levels, $n = 473$; Bray–Curtis similarity Index measure, permutation = 9999), and pairwise comparisons were made to ascertain differences among groups in the same depth ranges [49,50]. The SIMPER (SIMilarity PERcentage) test was performed to assess which taxa were primarily responsible for the observed differences [51]. All statistical analyses were carried out using PRIMER-e 7 version 7.0 with the PERMANOVA+ Add On package.

2.4. Most Common Species

The most frequent taxa were arbitrarily selected from the database, comprising those occurring in more than 25% of the total dives. More detailed investigations were conducted into these taxa. The semi-quantitative indications of the abundance of each taxon were used to build large-scale distribution maps. Maps were created using QGIS (version 3.38). Their depth ranges in each site of the present study and those reported in the available literature were used to build a comparative Box plot to visualise the concordance of the present records with the known depth ranges of the species.

2.5. Ecological Insight

30 to 130 frames per each of the selected taxa were collected to calculate their average and maximum density (number of individuals m⁻² $\pm$ SE) or coverage (%). The number of individuals and the covered surface (evaluated using the ROV laser beams) were calculated using ImageJ 1.53a

To assess the habitat preference of the target species, we noted the type and inclination of the substrate on which they were observed. The substrates were defined according to five categories: (M) mud, (D) detritic bottom (including sand to coarse-grained sediment, biogenic detritus, and rhodoliths), (R) outcropping rocks, (CCA) rocks covered by crustose coralline algae, and (ART) artificial (including marine litter and fishing gear). The inclina-

tion was divided into three categories: (H) horizontal (0–30°), (S) sloping (31–80°), and (V) vertical (81–90°). For each taxon, a semi-quantitative evaluation of preference was given using the 0–3 scale (never observed, 0; occasionally observed, 1; often observed, 2; most commonly observed, 3). Finally, the habitats where the target taxa were observed were defined according to the recently revised UNEP/SPA-RAC classification [15].

3. Results

3.1. Sponge Diversity

The analysis of the ROV footage allowed the identification of fifty-three taxa, of which fifty-one belonged to the class Demospongiae, one to Calcarea, and one to Homoscleromorpha (Table 1). Seven taxa were identified at the genus level; the group *Axinella damicornis/verrucosa* was created because these two species share a similar morphological aspect and are frequently observed in the same habitat, complicating their discrimination at the species level when based solely on ROV images. The putative actual diversity of large sponges in the mesophotic zone, calculated considering not only the taxa identifiable at the species/genus level but also the morphotypes, indicated that around 60% of the large sponges present in the mesophotic zone remain unidentified.

Table 1. List of the sponge taxa identified in the present work, with a separate percentage frequency of observation for the total dataset and each macro-area. In bold: taxa considered for more detailed analyses. Legend: LIG, Ligurian Sea; NCT, North–central Tyrrhenian Sea; ST, South Tyrrhenian Sea; SC, Sicily Channel; OR, offshore reliefs.

Sponge Taxon	Frequency (%)					
Demospongiae	TOT	LIG	NCT	ST	SC	OR
<i>Acanthella acuta</i> Schmidt, 1862	2.1	9.0	0.0	0.0	0.0	0.0
<i>Agelas oroides</i> (Schmidt, 1864)	18.0	44.1	6.6	8.2	24.6	10.0
<i>Aplysilla sulfurea</i> Schulze, 1878	0.4	0.0	0.8	0.5	0.0	0.0
<i>Aplysina cavernicola</i> (Vacelet, 1959)	26.1	57.7	23.8	14.2	8.8	20.0
<i>Axinella cannabina</i> (Esper, 1794)	1.0	0.0	1.6	1.6	0.0	0.0
<i>Axinella polypoides</i> Schmidt, 1862	10.1	29.7	6.6	0.0	14.0	0.0
<i>Axinella damicornis/verrucosa</i>	54.9	82.0	63.1	35.0	47.4	60.0
<i>Axinyssa digitata</i> (Cabioch, 1968)	0.4	0.0	0.0	0.5	1.8	0.0
<i>Calyx nicaeensis</i> (Risso, 1827)	1.7	1.8	0.0	1.6	5.3	0.0
<i>Chondrosia reniformis</i> Nardo, 1847	28.2	58.6	13.1	16.4	40.4	20.0
<i>Ciocalyptra penicillus</i> Bowerbank, 1862	1.0	0.0	0.8	0.5	3.5	10.0
<i>Cliona celata</i> Grant, 1826	0.4	0.0	0.0	0.0	0.0	20.0
<i>Cliona viridis</i> (Schmidt, 1862)	6.0	4.5	5.7	3.3	19.3	0.0
<i>Crella</i> (<i>Crella</i>) <i>elegans</i> (Schmidt, 1862)	11.4	4.5	7.4	5.5	12.3	0.0
<i>Crella</i> (<i>Grayella</i>) <i>pulvinar</i> (Schmidt, 1868)	6.4	32.4	2.5	6.0	8.8	0.0
<i>Dendrilla</i> sp.	0.8	0.0	0.0	0.0	7.0	0.0
<i>Dysidea avara</i> (Schmidt, 1862)	11.0	39.6	0.0	1.1	12.3	0.0
<i>Dysidea fragilis</i> (Montagu, 1814)	4.3	12.6	0.0	2.2	5.3	0.0
<i>Foraminospongia</i> spp.	33.3	4.5	64.8	27.9	33.3	70.0
<i>Geodia</i> sp.	0.2	0.0	0.0	0.0	0.0	10.0
<i>Haliclona</i> (<i>Gellius</i>) <i>bioxeata</i> (Boury-Esnault, Pansini & Uriz, 1994)	5.2	0.0	14.8	0.5	10.5	0.0

Table 1. Cont.

Sponge Taxon	Frequency (%)					
<i>Haliclona (Halichoclona) fulva</i> (Topsent, 1893)	9.5	1.8	7.4	12.6	8.8	0.0
<i>Haliclona (Halichoclona) magna</i> (Vacelet, 1969)	5.4	7.2	12.3	10.4	7.0	0.0
<i>Haliclona (Soestella) fimbriata</i> Bertolino & Pansini, 2015	8.1	0.9	21.3	10.4	19.3	0.0
<i>Haliclona (Soestella) implexa</i> (Schmidt, 1868)	11.8	0.9	4.9	8.7	5.3	0.0
<i>Haliclona (Reniera) mediterranea</i> Griessinger, 1971	8.1	3.6	11.5	6.0	17.5	0.0
<i>Haliclona poecillastroides</i> (Vacelet, 1969)	17.8	27.9	15.6	12.6	19.3	20.0
<i>Hamacantha (Vomerula) falcula</i> (Bowerbank, 1874)	5.0	1.8	9.8	3.3	3.5	20.0
<i>Hemimycale columella</i> (Bowerbank, 1874)	16.8	16.2	10.7	15.8	36.8	0.0
<i>Hexadella dedritifera</i> Topsent, 1913	14.5	7.2	23.0	14.8	12.3	0.0
<i>Hexadella racovitzae</i> Topsent, 1896	37.3	62.2	41.0	22.4	29.8	30.0
<i>Lycopodina hypogea</i> (Vacelet & Boury-Esnault, 1996)	0.8	0.0	3.3	0.0	0.0	0.0
<i>Pachastrella monilifera</i> Schmidt, 1868	7.0	2.7	20.5	0.5	0.0	50.0
<i>Petrosia (Petrosia) ficiformis</i> (Poiret, 1789)	11.8	28.8	2.5	6.6	17.5	0.0
<i>Phakellia</i> spp.	2.9	0.0	9.8	0.0	3.5	0.0
<i>Pleraplysilla spinifera</i> (Schulze, 1879)	12.8	19.8	6.6	11.5	17.5	10.0
<i>Poecillastra compressa</i> (Bowerbank, 1866)	10.8	3.6	32.0	1.1	1.8	60.0
<i>Polymastia polytylota</i> Vacelet, 1969	3.5	0.9	4.1	3.3	0.0	50.0
<i>Raspailia (Raspailia) viminalis</i> Schmidt, 1862	4.3	0.9	2.5	4.4	14.0	10.0
<i>Rhizaxinella</i> spp.	4.1	0.9	1.6	8.2	1.8	10.0
<i>Sarcotragus foetidus</i> Schmidt, 1862	18.2	68.5	2.5	2.2	8.8	0.0
<i>Spongia (Spongia) lamella</i> (Schulze, 1879)	12.2	41.4	1.6	2.2	12.3	0.0
<i>Stelligera stuposa</i> (Ellis & Solander, 1786)	0.2	0.0	0.8	0.0	0.0	0.0
<i>Suberites domuncula</i> (Olivi, 1792)	0.8	0.9	0.0	0.5	3.5	0.0
<i>Suberites syringella</i> (Schmidt, 1868)	5.2	0.0	3.3	8.7	7.0	10.0
<i>Tethya aurantium</i> (Pallas, 1766)	0.6	2.7	0.0	0.0	0.0	0.0
<i>Tethya citrina</i> Sarà & Melone, 1965	1.9	0.9	3.3	0.5	1.8	20.0
<i>Topsentia calabrisellae</i> Bertolino & Pansini, 2015	2.3	0.0	2.5	4.4	0.0	0.0
<i>Topsentia vaceleti</i> Kefalas & Castritsi-Catharios, 2012	3.3	0.0	0.0	7.1	1.8	20.0
<i>Ulosa digitata</i> (Schmidt, 1866)	1.2	5.4	0.0	0.0	0.0	0.0
<i>Weberella</i> sp.	2.7	0.0	4.1	2.2	7.0	0.0
<u>Calcarea</u>						
<i>Clathrina lacunosa</i> (Johnston, 1842)	5.6	0.9	9.0	2.2	15.8	20.0
<u>Homoscleromorpha</u>						
<i>Oscarella</i> spp.	15.3	29.7	10.7	12.0	10.5	0.0

3.2. Large-Scale Distribution

Some of the identified taxa showed a peculiar pattern of distribution. For example, the keratoses *Dysidea avara* (Schmidt, 1862), *Sarcotragus foetidus* Schmidt, 1862, *Spongia (Spongia) lamella* (Schulze, 1879), *Agelas oroides* (Schmidt, 1864), and *Crella (Crella) elegans* (Schmidt, 1862) were mainly present in the Ligurian Sea. On the other hand, *Hemimycale columella* (Bowerbank, 1874), *Haliclona (Soestella) fimbriata* Bertolino & Pansini, 2015, *Raspailia (Raspailia) viminalis* Schmidt, 1862, and *Topsentia vaceleti* Kefalas & Castritsi-Catharios, 2012

were typical southern species (Table 1). No species exclusive to a single macro-area were found (Table 1).

Differences among macro-areas were always significant in terms of sponge occurrence and dominance in the upper mesophotic zone (40–100 m), as confirmed by means of PERMANOVA ($p = 0.001$) (Table S1, Figure 1A).

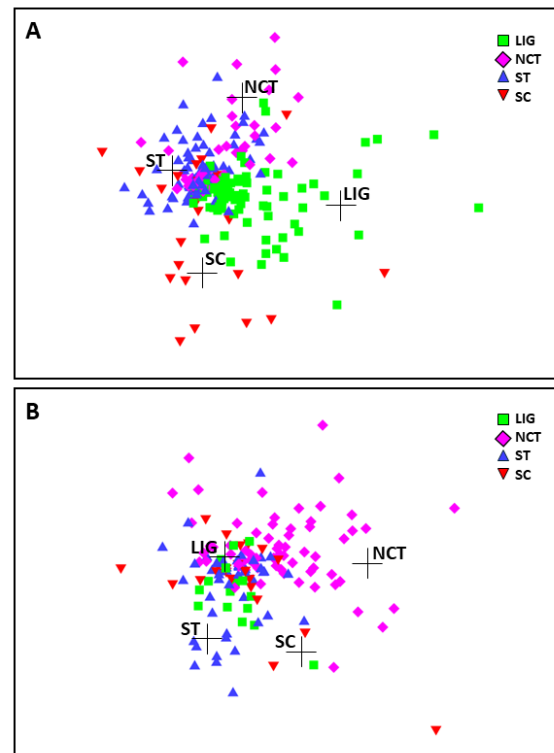


Figure 1. Non-metric Multi-Dimensional Scaling (nMDS) plots for the (A) upper (<100 m) and (B) lower (>100 m) mesophotic zone. Bray–Curtis similarity Index; Shepard plot stress plots: 0.015. LIG, Ligurian Sea; NCT, North–central Tyrrhenian Sea; ST, South Tyrrhenian Sea; SC, Sicily Channel.

Ligurian sites showed higher intra-similarity (37.4%), mainly due to the high frequency of occurrence of *Axinella damicornis/verrucosa*, *S. foetidus*, and *Chondrosia reniformis* Nardo, 1847. In comparison, the South Tyrrhenian Sea macro-area was the most heterogeneous (13.0% similarity), dominated by *A. damicornis/verrucosa*, *C. reniformis*, and *Hexadella racovitzai* Topsent, 1896 (Table S2). Among the macro-areas, the highest level of similarity was observed between the Ligurian Sea and the Sicily Channel (23.6%), decreasing to 21.1% between the Liguria Sea and the North–central Tyrrhenian Sea and reaching the minimum value of 15.0% when the Sicily Channel and the South Tyrrhenian Sea were compared (Table S2, Figure 2A).

In the lower mesophotic zone (100–200 m), the differences among the macro-areas remained significant (PERMANOVA, $p = 0.001$) (Table S1; Figure 1B). The similarity within each macro-area slightly decreased, except for the North–central Tyrrhenian Sea (from 23% in the upper mesophotic zone to 31.7% in the lower one). In contrast, the South Tyrrhenian Sea remained the most heterogeneous group (7.3%) (Table S3, Figure 2B).

Although the taxon contributions remained similar to those observed in the shallower depth range, *Foraminospongia* spp. showed a marked widespread presence and abundance in the deepest range, with percentage contribution values ranging from 35.8% in the Ligurian Sea to 54.4% in the North–central Tyrrhenian Sea (Table S3).

The average number of sponge taxa per site showed a peak in the Ligurian Sea (7.2 ± 0.4 taxa per dive) and a marked decrease moving southward, with the lowest value reported in the South Tyrrhenian Sea (3.2 ± 0.2 taxa per dive) (Figure 3A). A second peak

of average diversity was registered in the Sicily Channel (5.4 ± 0.6 taxa per dive), and a similar value was observed for the offshore reliefs (5.5 ± 1.2 taxa per dive) (Figure 3A).

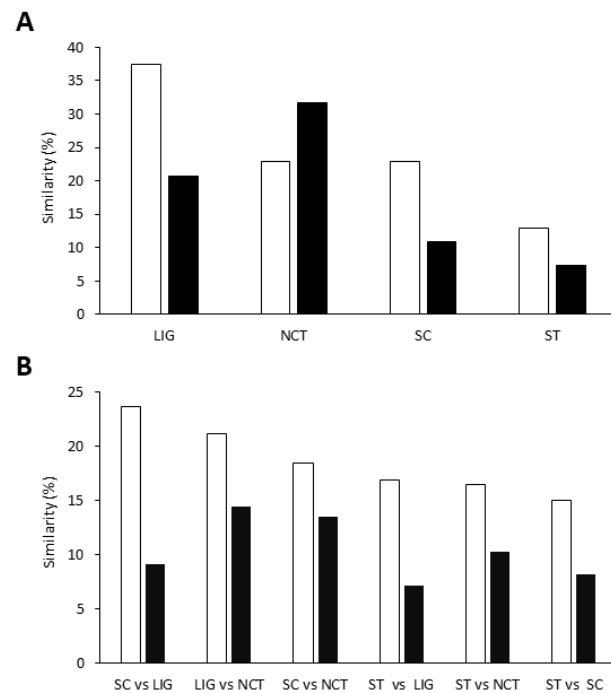


Figure 2. (A) Similarity percentage of each macro-area, and (B) pair-wise comparisons among macro-areas. White bars, upper (<100 m) mesophotic zone; black bars, lower (>100 m) mesophotic zone. LIG, Ligurian Sea; NCT, North-central Tyrrhenian Sea; ST, South Tyrrhenian Sea; SC, Sicily Channel.

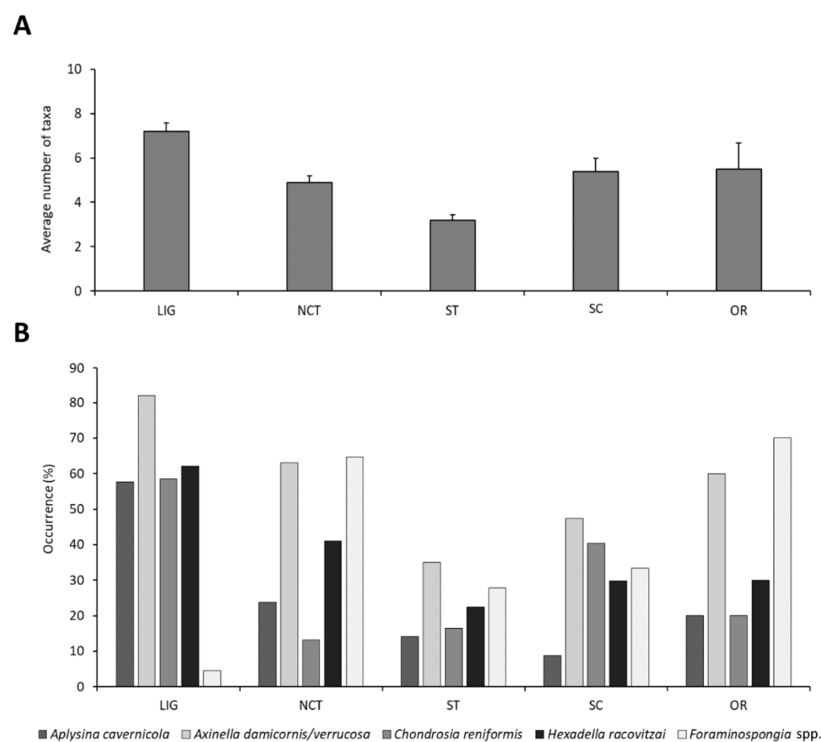


Figure 3. (A) Average number of sponge taxa ($\pm$ SE) in each site in the five considered macro-areas, and (B) percentage frequency of occurrence of the five target sponge taxa in each macro-area. Legend: LIG, Ligurian Sea; NCT, North-central Tyrrhenian Sea; ST, South Tyrrhenian Sea; SC, Sicily Channel; OR, offshore reliefs.

3.3. Most Common Species

Considering the total frequency of occurrence, 34 of the listed taxa were sporadically observed (in less than 10% of the sites), 14 were observed in between 10% and 25% of the sites, and only five were observed in more than 25% of the visited sites (Table 1). *Aplysina cavernicola* Vacelet, 1959, the group *Axinella damicornis/verrucosa*, *C. reniformis*, *Foraminospongia* spp., and *H. racovitzai* were the most common identifiable taxa, with *A. damicornis/verrucosa* present in about 55% of the explored sites, *H. racovitzai* in about 36%, *Foraminospongia* spp. in about 33%, and *A. cavernicola* and *C. reniformis* in about 27% (Table 1).

Considering the large-scale distribution of these taxa, four showed a pattern similar to that observed for the overall spongofauna, with a maximum in the Ligurian Sea (82% of the sites for *A. damicornis/verrucosa* and about 60% of the sites for the other taxa) and a progressive decrease moving southward in the Tyrrhenian Sea, with percentages of occurrence between 14% and 35% (Figures 3B and 4A–D). A second minor peak of occurrence in the Sicily Channel was reported for *A. damicornis/verrucosa*, *C. reniformis*, and *H. racovitzai* but not for *A. cavernicola*, which was present in only five sites in this macro-area (Figures 3B and 4A–D). In the North–central Tyrrhenian macro-area, all four taxa were observed in the Tuscan and Pontine archipelagos, sometimes with high abundances; on the other hand, along the eastern Sardinian coast, only *A. damicornis/verrucosa* and *H. racovitzai* were noted, while *A. cavernicola* and *C. reniformis* were virtually absent (Figure 4A–D).

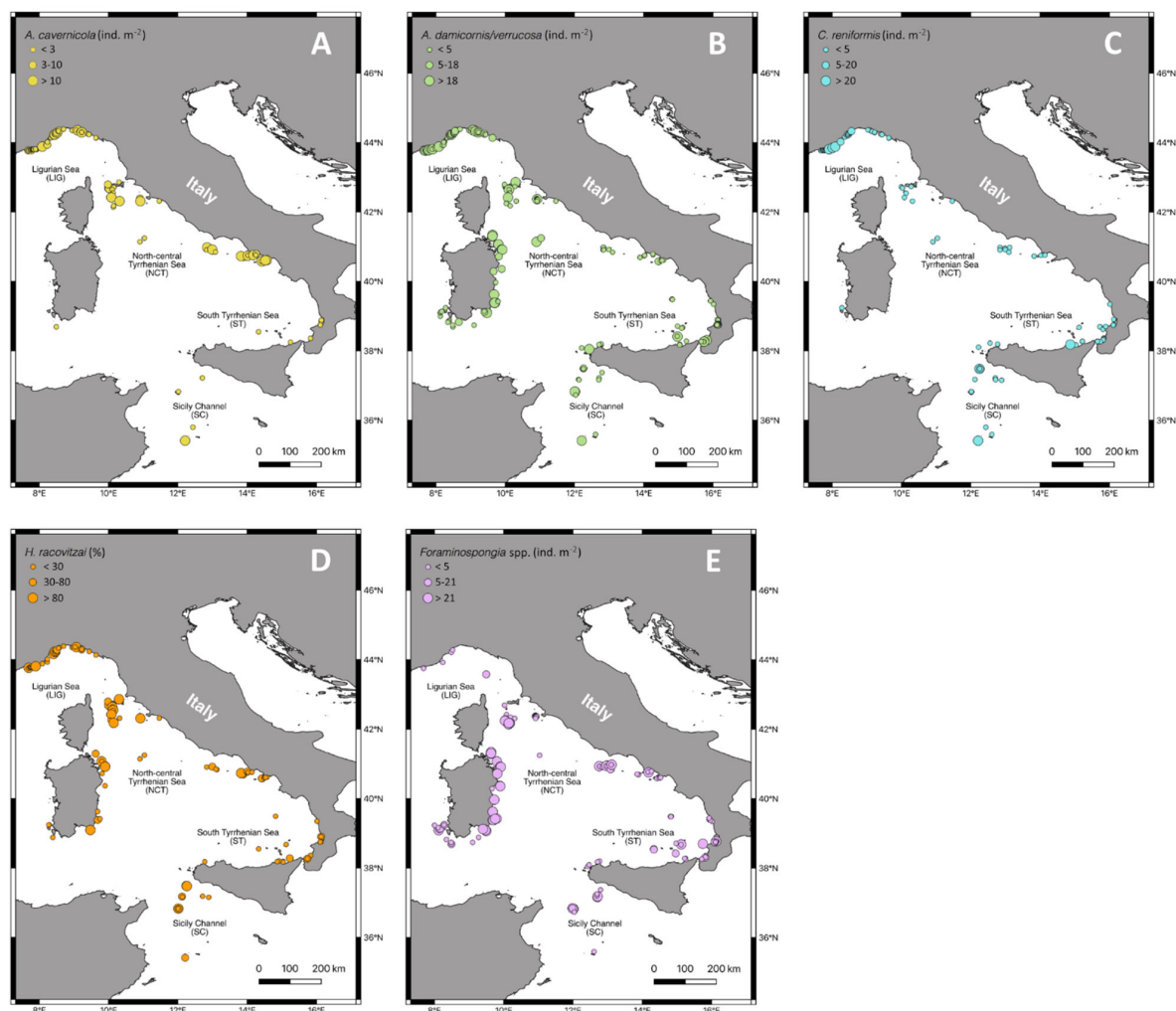


Figure 4. (A–E) Distribution maps of the populations of five target taxa, indicating the densities (number of individuals m^{-2} , percentage of coverage).

On the explored seamounts, these four taxa were observed on two upper mesophotic reliefs, Palinuro and Vercelli, in the Tyrrhenian Sea. In contrast, none were observed on the lower mesophotic Santa Lucia Seamount in the Ligurian Sea. In contrast, *Foraminospongia* spp. showed a peak of occurrence on the offshore reliefs, observed on all three mesophotic seamounts, and a second peak in the North-central Tyrrhenian Sea, especially along the Sardinian coast. At the same time, it was almost absent in the Ligurian Sea (Figures 3B and 4E).

Regarding the bathymetric distribution of these taxa, the recorded depth ranges were 40–140 m for *A. cavernicola*, 40–188 m for *Axinella damicornis/verrucosa*, 40–132 m for *C. reniformis*, 40–165 m for *H. racovitzai*, and 55–200 m for *Foraminospongia* spp. (Figure 5). The distribution medians from the literature of the four species were between 15 and 31 m, with the quartiles extending to the upper limit of the mesophotic zone (40 m). In the present dataset, the highest occurrence was observed between 70 and 80 m for *A. cavernicola*, *Axinella damicornis/verrucosa*, and *H. racovitzai*, and around 60 m for *C. reniformis* (Figure 5). Since *Foraminospongia* spp. was identified only at the genus level, no comparison could be made for this taxon (Figure 5).

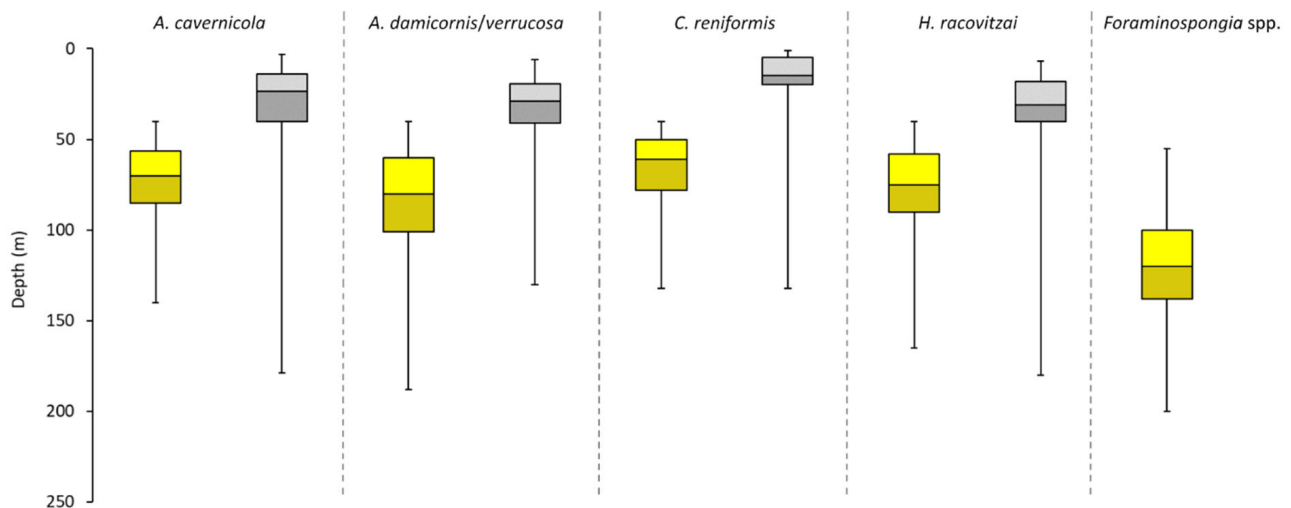


Figure 5. Bathymetric distributions of the five target taxa observed in the present work (yellow) and reported in the available literature (grey).

3.4. Ecological Insight

In numerous sites, very dense aggregations of each of the five taxa were observed (Figures 4 and 6): *A. cavernicola*'s mean density varied between 6.9 ± 1.1 and 26.1 ± 2.5 individuals m^{-2} , reaching a maximum of 42 individuals m^{-2} on the coralligenous outcrops of the Pontine Archipelago (North-central Tyrrhenian Sea) at a 70 m depth. On average, the density of *A. damicornis/verrucosa* was between 15.1 ± 1.4 and 26.8 ± 2.3 individuals m^{-2} , with a peak of 56 individuals m^{-2} on the silted rocky flanks of the Bordighera Canyon (Ligurian Sea) at around 80 m. The mean density of *C. reniformis* varied between 8.3 ± 1.8 and 37.7 ± 5.6 individuals m^{-2} on coralligenous and outcropping rocks, with a maximum of 77 individuals m^{-2} at 60 m in the Gulf of Gioiosa (South Tyrrhenian Sea). Finally, *Foraminospongia* spp.'s average density varied between 9.5 ± 1.6 and 37.2 ± 4.3 individuals m^{-2} , reaching the maximum density in Orosei Canyon (North-central Tyrrhenian Sea) at 172 m, with 86 individuals m^{-2} . The encrusting sponge *H. racovitzai* completely covered the rocks on which it was settled, as in the Ligurian site of Santo Stefano at around 90 m.

Regarding the habitat preferences of the five target species, none were observed on mud or artificial substrates (Figure 7). *A. cavernicola*, *A. damicornis/verrucosa*, *C. reniformis*, and *Foraminospongia* spp. were most frequently noted on outcropping and coralligenous rocks with low to medium inclination, even if they were also recorded on detritic bottoms, including rhodolith beds. *H. racovitzai* was reported exclusively on sloping and vertical hardgrounds and rocks covered by crustose coralline algae (Figure 7).

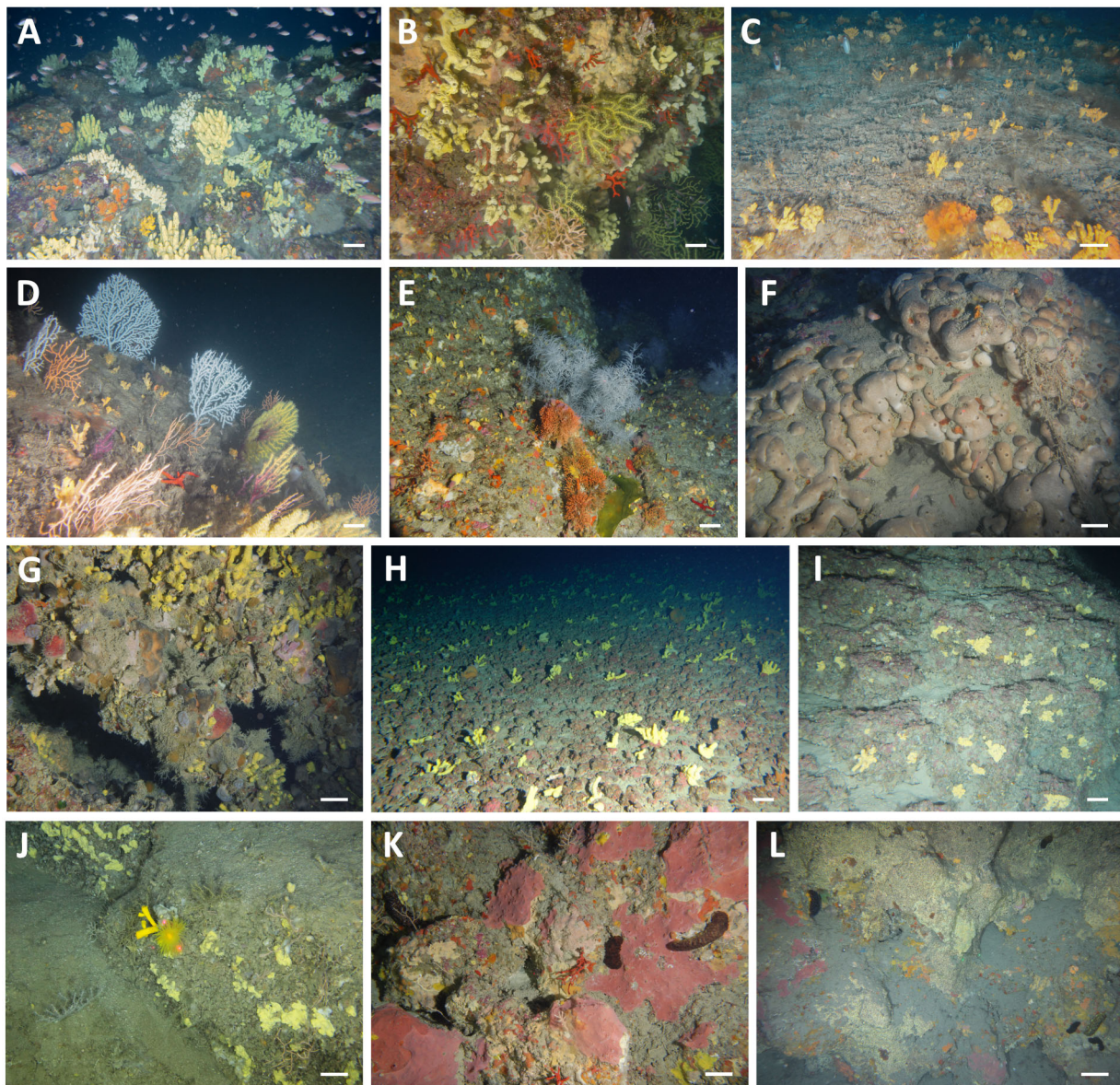


Figure 6. Aggregations of the five target taxa in different habitats: (A) numerous colonies of *Aplysina cavernicola* on the coralligenous outcrops in Diano Marina (western Ligurian Sea, 55 m); (B) *A. cavernicola* and *Hexadella racovitzai* dominating the basal layer of the facies with Alcyonacea on Ischia Island (South Tyrrhenian Sea, 75 m); (C) dense aggregation of *Axinella damicornis/verrucosa* on the detritic bottom of Santo Stefano (western Ligurian Sea, 50 m); (D,E) numerous individuals of *A. damicornis/verrucosa* beneath gorgonian and black coral forests, respectively (Bordighera Canyon, western Ligurian Sea, 75 m; Favazzina, South Tyrrhenian Sea, 85 m); (F) the densest aggregation of *Chondrosia reniformis* observed in the present study on the circalittoral coralligenous outcrops in the Gulf of Gioiosa (South Tyrrhenian Sea, 78 m); (G) *A. cavernicola* and *C. reniformis* together with other benthic organisms completely covering an iron shipwreck in Lampedusa (Sicily Channel, 65 m); (H) *Foraminospongia* spp. on a rhodolith bed in Porto Corallo (North–central Tyrrhenian Sea, 125 m); (I) dense aggregation of *Foraminospongia* spp. on coralligenous accretions in the Pontine Archipelago (North–central Tyrrhenian Sea, 105 m); (J) numerous specimens of *Foraminospongia* spp. together with structuring anthozoans on the offshore circalittoral rocks off Orosei Canyon (North–central Tyrrhenian Sea, 170 m); (K) bright reddish patches of *H. racovitzai* on a coralligenous cliff of Elba Island (North–central Tyrrhenian Sea, 85 m); (L) the silted deep banks of Santo Stefano covered by contracted *H. racovitzai* (western Ligurian Sea, 90 m). Scale bar: 10 cm.

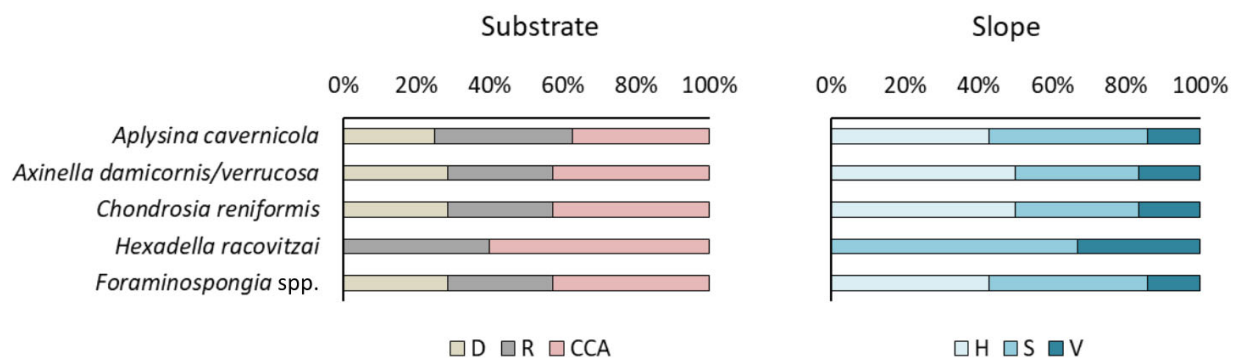


Figure 7. Percentage preference for the considered types of substrates (**left**) and slope (**right**) of the target taxa. Substrate categories' codes: D, detritic including rhodoliths; R, outcropping or sub-outcropping rocks; CCA, rocks covered by crustose coralline algae. Inclination category codes: H, horizontal or sub-horizontal; S, sloping; V, vertical or sub-vertical.

Finally, considering the recently revised SPA/RAC classification of Mediterranean benthic habitats, the five target species were observed in seven facies characterised by large and erect sponges on coralligenous outcrops, outcropping rocks and detritic bottoms. Five (MC1.512a, MC1.512b, MC1.521a, MC3.512, MC3.515) were in the circalittoral zone, one (MD1.512) in the offshore circalittoral zone, and one (ME1.512) in the upper bathyal zone, where they were already listed. In the present work, they were also reported in different habitats in the circalittoral and the offshore circalittoral zone as associated species of facies dominated by invertebrates, including cnidarians and brachiopods, sometimes with very high densities (Figures 6 and 7).

4. Discussion

Sponges are among the most common suspension feeders in marine benthic ecosystems from intertidal to bathyal depths [52]. Nevertheless, information about their diversity, distribution, and ecology below 40 m depth is minimal. This work represents the first attempt to characterise the mesophotic massive spongofauna along the Italian coast from a large-scale geographic (600 NM latitudinal gradient) and bathymetric (40–200 m depth) perspective. The ROV imaging technique identified fifty-three taxa (87% at the species level), confirming the mesophotic zone as a rich biodiversity hotspot [53].

All the identified taxa were already reported in the Mediterranean Sea and represent 10.5% of the species known in the Italian seas [54,55]. This percentage must be considered partial since we considered only large sponges visible through ROV footage thriving below 40 m depth, excluding small, cryptic taxa and those living in shallow waters.

Among them, eight (namely, *A. oroides*, *A. cannabina*, *C. nicaeensis*, *H. (G.) bioxeata*, *H. (H.) magna*, *H. (S.) fimbriata*, *T. calabrisellae*, and *T. vaceleti*) are endemic to the Mediterranean Sea. *A. cavernicola*, *A. cannabina*, *A. polypoides*, *L. hypogea*, *S. foetidus*, *S. lamella*, *T. aurantium*, and *T. citrina* are included in international protection lists, specifically in the Annexes II of the Bern and Barcelona Conventions because of their scattered geographic distribution and possible reduction owing to the impact of anthropic activities and the effects of climate change [56–61].

The difficulty in identifying Porifera through ROV footage has led to underestimating the actual diversity value. A tentative estimation of the actual sponge diversity accounted for more than double the identified species, and this datum indeed remains underestimated because of the small, cryptic species [47]. On the other hand, this technique allowed us to observe live sponges in their natural habitat, defining their presence and abundance in mesophotic environments. A similar difficulty was also highlighted for heterobranchs, though the colouration patterns and stenophagy of the visible species were a significant help in identification [31].

A. cavernicola, *Axinella damicornis/verrucosa*, *Chondrosia reniformis*, and *Hexadella racovitzae* were the most frequently observed identifiable taxa. In addition, *Foraminospongia* spp. was highly common in the dataset. This latter genus was recently described as including two new species, *F. balearica* (Díaz, Ramírez-Amaro & Ordines, 2021) and *F. minuta* (Díaz, Ramírez-Amaro & Ordines, 2021), collected at mesophotic depths on three seamounts in the Mallorca Channel [41]. *F. minuta* is a small (about 1.5 cm in diameter and 0.5 cm high), massive-encrusting sponge, greyish in colour, living on hard bottoms associated with fossil ostreid reefs. On the other hand, *F. balearica* is a large (up to 6 cm in diameter, with tubes up to 2–3 cm high), massive-tubular, golden-yellow sponge mainly found on rhodolith beds and sedimentary bottoms. This latter species appears very similar to the sponge observed in over 160 sites visited in the present study, sometimes forming very dense aggregations. Moreover, a single specimen collected in the Pontine Archipelago (North–central Tyrrhenian Sea) was formally identified as *F. balearica* based on spicule analysis. Nevertheless, since we could not exclude the presence of different species of the same genus, the taxon *Foraminospongia* spp. was created conservatively.

Overall, the mesophotic sponge diversity presented two main peaks in the Ligurian Sea and the Sicily Channel, with a significant reduction in the Tyrrhenian Sea, especially in the southern sector, and a high diversity on the explored offshore reliefs. Several biotic and abiotic factors may determine this distribution. The high diversity recorded in the Ligurian Sea agrees with the findings of vast and dense sponge grounds dominated by the massive keratose sponge *S. foetidus* along the western Ligurian coast between 40 and 70 m in depth [45], as well as two sponge-dominated communities, with a high abundance of *Axinella* spp. and *Haliclona* cf. *mediterranea*, together with several other species, including *A. cavernicola*, *A. polypoides*, *C. reniformis*, *H. racovitzae*, and some unidentified sponges [40]. This sponge abundance was hypothesised as being driven by a peculiar set of environmental features favouring filter feeders [40,45]. Indeed, the Ligurian basin shows a high sedimentation rate and elevated organic inputs deriving from the several rivers flowing from the Alpine and the Apennine chains and from the main cyclonic circulation associated with the northerly winds, causing the upwelling of deep water along the canyons [45,62,63]. These factors may explain the high sponge biomass observed by Enrichetti et al. [45], the high biodiversity reported in this study, and, indirectly, the high occurrence of specialised sponge predators such as heterobranchs [31]. *C. reniformis* incorporates foreign material suspended in the water column, such as sand grains and sponge spicules, to construct its skeleton [64]. The high sedimentation rate of the Ligurian Sea may favour the presence of this species, explaining the high abundance observed in this area. The same factor may determine the virtual absence of *C. reniformis* along the eastern Sardinian slope canyon system [65]. The rocky flanks of the canyons, exposed to turbulent hydrodynamic conditions, may disadvantage the settlement of this species. *Foraminospongia* spp. showed an opposite distribution: rare in the Ligurian Sea and abundant in the North–central Tyrrhenian Sea. *Foraminospongia* spp., observed mainly on rhodolith beds and inclined hard substrates, may prefer habitats with strong water currents and low levels of sedimentation, such as the two cited [65,66]. Nevertheless, the ecology of this recently described taxon requires further investigation to pinpoint the factors driving its distribution.

The second sponge hotspot identified in this study is located in the Sicily Channel (hosting 77.4% of the total sponge richness). The Sicily Channel, a crossroad between the western and the eastern Mediterranean basins, is characterised by peculiar geomorphologic and oceanographic characteristics, making it one of the most important biodiversity hotspots in the Mediterranean Sea [67–69]. Its geomorphology includes several submarine reliefs (e.g., banks, ridges, knolls, pinnacles, and seamounts) composed of sedimentary or volcanic rocks. The hydrodynamic circulation is dominated on the surface by the inflow of the Modified Atlantic Water (MAW) from the West, at intermediate depth by the outflow of the Levantine Intermediate Water (LIW) flowing from the eastern basin, and on the bottom from the Mediterranean Deep Water (MDW) [67,70–72]. These main currents, in synergy with seasonal local winds, mesoscale structures, and the complex seafloor topog-

raphy, contribute to making this area one of the most productive in the Mediterranean Sea [70,73–77]. Several studies have already reported the high bento-nektonic biodiversity in the region [69,72,75,78,79]. Regarding Porifera, numerous studies revealed a noticeable sponge occurrence in the Sicily Channel [34,54,80–82]. Some authors highlighted the large variety of sponges inhabiting the deep water around the Maltese Islands (Strait of Sicily) between 50 and 1000 m, reporting 20 and 23 species, respectively [83,84].

To emphasise the nutrients as a key factor driving the diversity and abundance of the sponge community in the Ligurian Sea and Sicily Channel, the trophic levels of different areas of the Tyrrhenian basin characterised by average Chl-a concentrations should be considered. The Mediterranean Sea is classified as an oligotrophic basin, as its primary production by autotrophs is generally weak, and Chl-a concentration in the open ocean areas rarely exceeds $2\text{--}3\text{ mg m}^{-3}$ [85]. Although high Chl-a values over large areas are seldom detected in the basin, an important exception is represented by large blooms observed in the Ligurian–Provençal Region. From this basin, the parameter progressively decreases from the northern Tyrrhenian basin to the southern one [86]. A slight increase in productivity can be observed in the Sicily Channel [86].

An alternative or complementary explication of these two peaks arises from the biogeographic distribution of Atlantic fauna in the Mediterranean Sea. According to Sitjà [85], the Atlantic spongofauna entering the Mediterranean Sea disperses following two main superficial flows, one running northward through the Balearic Sea to the Ligurian basin and a second one bordering the northern African coast and reaching the Sicily Channel [85]. Following this observation, Sitjà supported a similarity between the deep-shelf sponge fauna of the Alboran Sea and that reported in the easternmost areas of the western Mediterranean Sea, such as the Ligurian Sea and the Sicily Channel [84]. In addition, Astraldi and Gasparini [87] and Astraldi et al. [88] claimed that the Tyrrhenian Sea can be considered the most isolated basin in the western Mediterranean Sea because of the shallow sill of the Corsica Channel to the North and that between Sicily and Sardinia to the South. By contrast, the other Italian seas exhibit more similarities with the rest of the Mediterranean basin. This scenario agrees with the clustering analysis presented in this study.

A high sponge diversity was observed on the mesophotic top of the visited seamounts, characterised by a flourishing offshore coralligenous habitat [7,89,90]. This datum must be treated cautiously due to the limited number of dives in these localities, which may have biased the overall diversity value. Unlike other previously investigated megabenthic groups (such as brachiopods) [31], none of the identified taxa showed a preference for seamounts. Nevertheless, several studies support the wide diversity of the spongofauna on offshore reliefs, probably related to the current conditions and inclination of the flanks that affect the sedimentation rates locally. These, in turn, favour active suspension feeders and, in some cases, contribute to the lower impact of fishing activities on coastal zones [17,24,41,89,91].

None of the identified species were observed exclusively in one macro-area. On the contrary, two species, namely, *Haliclona poecillastroides* (Vacelet, 1969) and *Polymastia polytylota* (Vacelet, 1969), which were previously reported as being exclusive to the Ligurian Sea and the North–central Tyrrhenian Sea, respectively, were observed in other areas in the present study, suggesting that their geographic distribution is larger than previously known [55].

The bathymetric distributions reported in the present work for the target taxa (excluding *Foraminospongia* spp.) agreed with those reported in the available literature, except for *A. damicornis/verrucosa*, whose maximum known depth is 130 m (*A. damicornis*, *A. polypoides*, and *A. verrucosa*, considered as a single taxon) [46]. These sponges were known in the mesophotic zone but are mainly reported in shallow waters, where they have been more intensively studied. The present study suggests that they might show their actual peak of occurrence at mesophotic depths down to the limit of the continental shelf, probably exploiting the lower competition levels with the photosynthetic community. A similar situation was recently observed for heterobranchs; the intense investigation at mesophotic depths

extended the known distribution ranges of most of the shallow-water species [32]. Following the bathymetric distribution reported for *F. balearica* (100–433 m) [41], *Foraminospongia* spp. was noted mainly in the deepest part of the mesophotic zone (100–145 m), with the lowest individuals observed at 437 m on the Baronie Seamount (North–central Tyrrhenian Sea, unpublished data). The similar geographic and bathymetric distributions and similar external morphology support the possibility that the species we encountered belongs to the same Balearic species.

Although the five target taxa have been largely studied, only a handful of papers report density values at mesophotic depths. The values found in the present study for *A. cavernicola* were higher than those observed in the Balearic Islands between 72 and 228 m in depth (5 ± 4.9 individuals m^{-2}) and in the Ligurian Sea between 30 and 80 m (1.51 ± 2.3 individuals m^{-2}) [10,40]. In the same Spanish localities, the average density of *A. damicornis/verrucosa* was ten times lower (2.4 ± 2.5 individuals m^{-2}) [10] than that noted in some Italian sites in the present study. Enrichetti et al. [40] reported densities of up to 25 individuals m^{-2} in the Ligurian Sea between 28 and 83 m. No specific studies have been conducted on the abundance of *C. reniformis* and *H. racovitzai* at mesophotic depths; nevertheless, both taxa were extensively investigated in shallow waters. In both cases, similarities were reported between the depth ranges. The densities of *C. reniformis* reported on sublittoral cliffs at 30–40 m in the Aegean Sea (between 1 ± 0.6 and 13 ± 2.2 individuals m^{-2}) [92] were comparable with those observed here. In the highly eutrophic North Adriatic Sea, *C. reniformis* is one of the most common and largest sponge species, with individuals larger than one square metre, covering up to 55% of the rocky substrate on which they settle between 5 and 7 m [93].

In shallow waters, *H. racovitzai* covers a high percentage of the walls and ceilings of submarine caves where it lives, sometimes even overgrowing other invertebrates [57,94]. Similarly, this species maintains its encrusting habitus at greater depths, sometimes completely covering the deep circalittoral outcropping rocks on which it settles. Finally, since *Foraminospongia* spp. was identified only at the genus level, a proper comparison with other studies was impossible. Nevertheless, a mean density of 6.2 ± 6.5 individuals m^{-2} with a maximum of 43 individuals m^{-2} was reported for *F. balearica* on the deep continental shelf of the Menorca Channel [10]. The values reported for *Foraminospongia* spp. along the Italian coast were generally higher, and the maximum abundance was twice that reported in the Balearic area.

Following the ecological knowledge reported in the literature, it is unsurprising that the five target species showed high variability in terms of the substrates on which they were settled, being observed on both horizontal detritic bottoms and inclined and sub-vertical hardgrounds. *A. cavernicola*, *A. damicornis/verrucosa*, *C. reniformis*, and *H. racovitzai* are mentioned in the recently revised SPA/RAC classification Manual of Mediterranean benthic habitats as typical components or associated species in numerous facies, mainly in the infralittoral zone [15]. *A. cavernicola* and *A. damicornis/verrucosa* are also cited in different habitats in the circalittoral and offshore circalittoral zones, including coralligenous cliffs, submarine caves, rocks covered by sediment and colonised by invertebrates, and coarse detritic bottoms, while *C. reniformis* and *H. racovitzai* are reported only on the walls and roofs of submerged caves in the circalittoral zone despite also being known to inhabit coralligenous and outcropping rocks [39,42,46,95]. The present study greatly expands the information available on the habitat occupied or formed by these taxa, such as deep coralligenous outcrops in association with cnidarians and brachiopods and offshore invertebrate-dominated rocks, where they may become dominant components of the benthic community. *Foraminospongia* spp. is cited as a typical taxon characterising the facies with large and erect sponges in the invertebrate-dominated upper bathyal rock [15,41]. Along the Italian coast, this taxon was also observed on mesophotic rhodolith beds, circalittoral coralligenous rocks and offshore circalittoral rocks, in association with large and erect sponges, Alcyonacea, Antipatharia, and Scleractinia. This information may be useful for the future implementation of the manual, providing a more complete overview of the

habitat preferences of the investigated taxa and establishing a basis for better conservation strategies.

5. Conclusions

The Mediterranean Sea is experiencing rapid environmental variations due to climate change. Marine sponges are particularly sensitive, modifying their communities in different ways. For example, in the 1980s, an intensive mass mortality event caused by a disease induced by a bacterium destroying spongin fibres affected keratose sponges, particularly those of the genus *Spongia* [96]. On the Portofino Promontory, quantitative and qualitative monitoring of the shallow-water sponge community showed different patterns for the considered taxa, with some more abundant now than in the past (*Axinella* spp. and *Agelas oroides*), some virtually stable (*Cliona viridis* and a complex of red encrusting sponges), and others drastically depleted (*Chondrosia reniformis*, *Phorbas tenacior* (Topsent, 1925), *Acanthella acuta*, *Ircinia* spp., *Dysidea avara*, and *Petrosia (Petrosia) ficiformis* [63]. At present, data on the composition and distribution of the mesophotic sponge communities at the basin scale are scant. The information reported in this paper, presenting an overview of the sponge diversity, distribution, and ecology in the Italian seas, is crucial for a comprehensive understanding of the mesophotic spongofauna and constitutes a baseline for future studies and conservation actions.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/jmse12112110/s1>, Figure S1. Map of the study area. Black dots indicate the coastal explored sites, and red dots indicate the visited offshore seamounts. Table S1. One-way PERMutational ANalysis Of VAriance (PERMANOVA) tests and pair-wise comparisons performed on the whole species matrix for upper (40–100 m) and lower (100–200 m) mesophotic depth ranges. Significant values are reported in bold. (Bray–Curtis similarity index; permutations: 9999). Table S2. Similarity percentage (SIMPER) test for the sponge taxa derived by means of ROV video transect analysis in the lower (100–200 m depth) mesophotic zone. Cut off at 70% of the cumulative contribution. Species with a percentage contribution within each macro-area greater than 10% and 5% between pair-wise comparisons are in bold. Table S3. Similarity percentage (SIMPER) test for the sponge taxa derived by means of ROV video transect analysis in the upper (40–100 m depth) mesophotic zone. Cut off at 70% of the cumulative contribution. Species with a percentage contribution within each macro-area greater than 10% and 5% between pair-wise comparisons are in bold.

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