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Sponges as Habitat Formers on Mesophotic, Soft-Substrate Seafloors of the Eastern Mediterranean

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Abstract

This study aims to investigate the ecological role of sponges as habitat formers on soft-bottom habitats of the mesophotic zone. As habitat formers, sponges significantly enhance benthic habitat complexity and establish associations with a plethora of organisms consequently augmenting local biodiversity. This role becomes particularly critical in areas subjected to intensive bottom trawling, where sponges often comprise a substantial portion of the discarded material. The examination of 114 massive sponge specimens, belonging to 10 sponge species, which were collected as bycatch from bottom trawls in the Aegean and Ionian ecoregions, revealed a total of over 4600 associated individuals of 78 invertebrate taxa, with crustaceans, mollusks, and polychaetes being the dominant groups. The composition of sponge-associated communities showed strong similarities to previously reported cases from shallow water hard substrates of the eastern Mediterranean, while displaying host-specific differences likely influenced by sponge morphology. Although depth did not significantly affect species richness, Shannon diversity, or evenness, a decrease in abundance of associated invertebrates was observed in deeper samples, suggesting a depth-related pattern that deserves further investigation. By forming stable substrate "islands" in otherwise unstable soft substrate environments, sponges play a vital role in structuring benthic communities. Their removal through bottom trawling not only results in the loss of the sponges themselves, but also disrupts the diverse communities they support. We suggest that sponge-associated fauna should be recognized as part of the discarded bycatch and emphasize the need for broader assessments of sponge-mediated biodiversity across similar Mediterranean habitats to support effective management and conservation strategies.

Keywords: sponge-associated fauna; benthic biodiversity; trawl impact; vulnerable marine ecosystems; eastern Mediterranean; MEDITS

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1. Introduction

The functional role of sponges (phylum: Porifera) in the marine environment is considered of great importance [1,2], as these organisms can significantly influence the composition of benthic communities [3,4]. Due to their complex morphology and ecological interactions, they have been characterized as "living hotels" [5,6], "ecosystem engineers" [7], and "habitat formers" [8]. These designations are based on their body structure, which provides habitat for a wide variety of associated taxa, from microorganisms to invertebrate and vertebrate animals, leading to diverse relationship types among host sponges and their associates. The complex three-dimensional structure of sponges—an intricate network of cavities and canals—provides suitable habitat for various macrobenthic species, which find protection, food, breeding space, and nursery areas [8], thus creating a community within a broader one. In some cases, the relationships are obligate, such as those of the *Synalpheus* shrimps which are exclusive symbionts of sponges [9].

Despite their well-documented ecological importance, sponge assemblages still remain understudied in areas subjected to fishing activity. Recent findings from trawlable soft-bottom habitats in the Aegean and Ionian ecoregions (Mediterranean Sea) revealed a remarkable diversity of sponge taxa [10], raising questions on their associated fauna. This associated fauna represents a form of "hidden biodiversity" that is removed from the mesophotic bottoms as incidental catch, augmenting the extent of fishing impact on these habitats.

Although sponge-associated communities in the eastern Mediterranean basin are well studied, research primarily focuses on shallow rocky bottoms [11–16] and on the hard substratum of submarine caves [5]. More recently, three publications appeared on the role of sponges as habitat formers in the Levantine Basin, two in the mesophotic zone of Israeli coasts [6,17] and one on the trawlable seafloors of Cyprus [18].

Recognizing this knowledge gap on the role of sponges in mesophotic soft-substrate habitats—particularly those impacted by bottom trawling—we collected sponges during field surveys with experimental and commercial bottom trawls in the Aegean and Ionian ecoregions, in the framework of three monitoring programs (mainly MEDITS Project). In this study, we explore the invertebrate diversity associated with selected sponge species, collected from soft-substrate, mesophotic habitats, most of which are exploited by bottom trawling. The following hypotheses were investigated: (a) sponges act as habitat formers in the soft bottoms of the mesophotic zone, hosting rich invertebrate communities; (b) different invertebrate communities inhabit different species of host sponges; and (c) depth influences the composition of the sponge-associated communities.

2. Materials and Methods

2.1. Study Area

Field surveys were conducted using both experimental and commercial bottom trawls in the soft mesophotic bottoms of the Aegean Sea and the eastern Ionian Sea, at depths between 20 and 200 m (Figure 1). Sponge material was collected as part of fish-stock monitoring programs carried out between 2016 and 2018. The sampling scheme and methodology are described in detail in Stamouli et al. [10].

2.2. Sampling and Sample Processing

Ten sponge species were selected for the study of their associated fauna: *Aplysina aerophoba* (Nardo, 1833), *Dysidea avara* (Schmidt, 1862), *Fasciospongia cavernosa* (Schmidt, 1862), (Linnaeus, 1767), *Ircinia variabilis* (Schmidt, 1862), *Suberites domuncula* (Olivi, 1792), *Suberites ficus* (Johnston, 1862), *Spongia (Spongia) officinalis* Linnaeus, 1759, *Scalarispongia scalaris* (Schmidt, 1862), and *Sarcotragus foetidus* Schmidt, 1862. These species were chosen among a total of 87 species found [10], based on their massive or tubular growth forms, characterized by a rich network of cavities and canals capable of supporting both infaunal and epifaunal organisms. In addition, most of these sponges have been documented previously as habitat formers in various marine environments, particularly on shallow rocky substrates (e.g., [12,13]). A total of 114 sponge specimens were collected from depths ranging between 20 and 200 m (Table 1). Of these, 73 specimens, representing nine species, were obtained from the 20–50 m depth zone, while 41 specimens representing eight sponge species were collected from the 50–200 m zone.

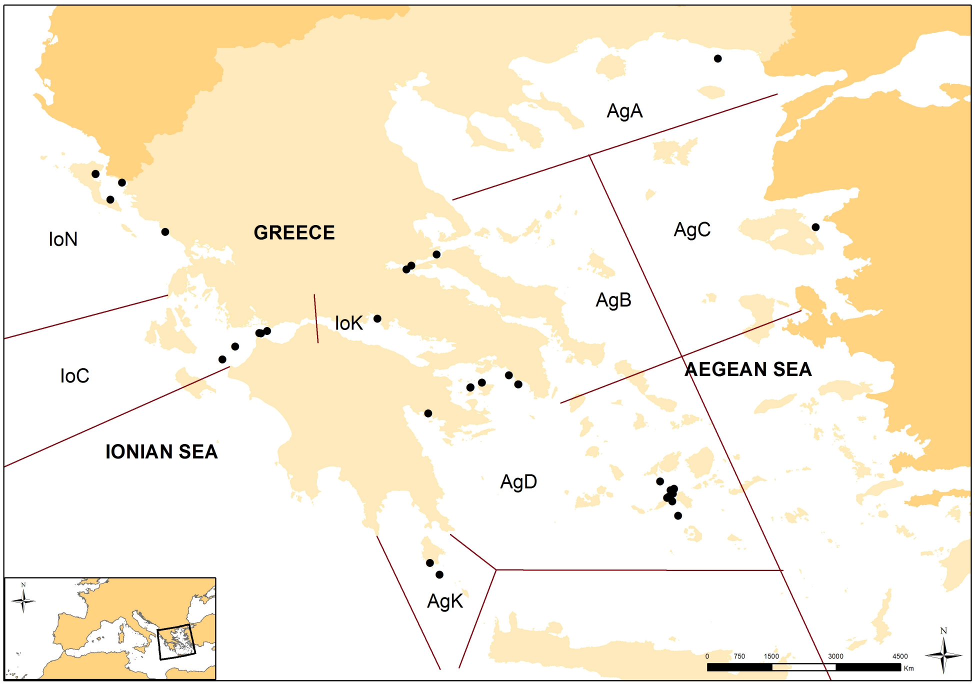

Figure 1. Map of the sampling stations (black dots) from which the sponge samples were caught during bottom trawl surveys. Bottom left corner: the location of the study area (Aegean and Ionian Seas) in the Mediterranean Sea. AgA—North Aegean; AgB—Central–West Aegean; AgC—Central–East Aegean; AgD—South–West Aegean; AgK—the marine area around Kythira Isl.; IoN—North Ionian; IoC—Central Ionian; IoK—the Korinthiakos gulf.

Table 1. Sponge species examined and number of specimens collected per subarea and depth zone.

	AgA	**AgB**	**AgC**	**AgD**	**AgK**	**IoN**	**IoC**	**IoK**	**20–50 m**	**50–200 m**
Aplysina aerophoba		5	1	4		2			6	6
Dysidea avara			2	3		1			6	1
Fasciospongia cavernosa			2	1					3	–
Geodia cydonium	1	1	2						4	–
Ircinia variabilis				15					12	3
Sarcotragus foetidus			10	23	4		3		22	18
Scalarispongia scalaris			2	2			1		2	3
Spongia (Spongia) officinalis				2		2	1		3	2
Suberites domuncula			15				3		15	3
Suberites ficus			2				2	1	–	5
Grand Total	1	6	36	50	4	5	10	1	73	41

Immediately after trawl retrieval, sponge specimens were carefully isolated in plastic bags to minimize the loss of epibionts or endobionts, and were subsequently stored frozen. The recommended sampling practice to isolate sponges in bags prior to detachment from the substrate to prevent loss of associates [5,11] was not feasible in our case due to the sampling procedure employed. However, Goren et al. [6] demonstrated that no significant difference exists in the number and abundance of associated species between samples of the same sponge species collected with coverage before detachment and those isolated after transport to the vessel. Therefore, we consider that the data obtained with our sampling method can be used for analyses and comparisons, still with caution.

Before processing, sponges were kept out of the freezer to reach room temperature. Then they were wet weighted and volumetrically measured using the water displacement method [6,11,16]. Specifically, after being weighed, each sponge specimen was submerged individually in an open plastic container filled with water up to the overflow point; the water displaced by the immersion was collected in a graduated measuring cylinder and its volume was recorded.

Sponges were subsequently dissected into small pieces along their canals and cavities using a scalpel, to minimize damage of the associated organisms (Figure 2). During dissection, organisms larger than 1 mm were collected and preserved by higher taxonomic group in 70% ethanol. Additional organisms retrieved from the water used during sponge rinsing and water displacement procedures were also collected and preserved using the same method.

Figure 2. Characteristic endobionts observed during removal from sponge specimens: (**a**) the shrimp *Synalpheus gambarelloides* (Nardo, 1847) in cavities of *Fasciospongia cavernosa*; (**b**) the crustaceans *Pilumnus spinifer* H. Milne Edwards, 1833 and *Cymodoce truncata* Leach, 1814 and a polychaete inhabiting cavities of *Sarcotragus foetidus*; (**c**) the ophiuroid *Ophiothrix fragilis* (Abildgaard in O.F. Müller, 1789) in cavities of *Scalarispongia scalaris*; and (**d**) the mollusk *Hiatella arctica* (Linnaeus, 1767) within cavities of *Ircinia variabilis*, (**e**) a polychaete in cavities of *Ircinia variabilis*, and (**f**) isopods inhabiting the internal cavity of the sponge *Sarcotragus foetidus*.

All the collected associated organisms were identified to the lowest possible taxonomic level. For each sponge specimen, the total abundance of associated individuals was recorded. To facilitate comparisons across sponge specimens of different size, the abundance of each associated taxon was standardized by calculating the number of individuals per liter of sponge volume. Taxonomic classification and nomenclature of associated fauna followed the World Register of Marine Species [19].

2.3. Data Analysis

To assess the composition of sponge-associated communities, we considered several community parameters. For each sponge specimen, we calculated the number of associated taxa (S), the abundance of associates per liter of sponge volume (A), the Shannon diversity index (H′), and the Pielou evenness index (J′). For each associated taxon we calculated: presence (P)—the number of sponge specimens in which the taxon occurred; frequency (F)—percentage presence of the taxa across all sponge specimens; abundance (As)—number of individuals per liter of sponge volume; and mean dominance (mDa)—the percentage of taxa abundance in relation to the total abundance of all associates.

To investigate differences in associated community composition among sponge species and depth zones, abundance data were log-transformed using the formula ((log x) + 1) to reduce the influence of dominant taxa. The transformed data were then used to construct a similarity matrix, comparing all possible pairs of samples, using the Bray–Curtis similarity index. Community patterns were visualized using Canonical Analysis of Principal Coordinates (CAP), performed in PRIMER v6 software.

Statistical differences in taxa richness, diversity, evenness, and abundance of associated fauna among sponge species were tested using one-way Analysis of Variance (ANOVA). To identify the key taxa contributing most to dissimilarities among sponge species, a Similarity Percentages (SIMPER) analysis was carried out. Additionally, the potential relationship between sponge volume and taxa richness, abundance, and diversity (expressed as Shannon index H′) was examined using the Spearman correlation coefficient (rho).

In order to compare the associated community composition across the same sponge species collected from different sampling subareas (Figure 1), PERMANOVA analysis was carried out for every sponge species separately. For the comparison of the associated community composition across depth zones, analysis was restricted to two sponge species, *Aplysina aerophoba* and *Sarcotragus foetidus*, for which at least five specimens were available from both the depth zones (20–50 m and 50–200 m).

3. Results

The volume of sponge specimens analyzed ranged from 8 to 7200 mL. The number of associated taxa varied among the different sponge specimens and ranged from 1 to 16. In 25.4% of the sponge specimens, only a single associated taxon was recorded, while 14.9% of the specimens hosted four taxa and 36% of the sponge specimens harbored more than five taxa each. A complete list of all sponge specimens examined along with information on depth of collection, wet weight, volume, number of associated taxa (S) and number of individuals (N) in each sample, is provided in Appendix A (Table A1).

3.1. Associated Macrofauna

A total of 4677 individuals of associated invertebrates were recorded, classified into 78 taxa (Table 2) and belonging to six higher taxonomic groups: Porifera, Crustacea, Mollusca, Polychaeta, Sipuncula, Echinodermata, and Ascidiacea.

Table 2. Taxa associated with the studied sponge species. Aa: *Aplysina aerophoba*; Da: *Dysidea avara*; Fc: *Fasciospongia cavernosa*; Gc: *Geodia cydonium*; Iv: *Ircinia variabilis*; So: *Spongia (Spongia) officinalis*; Ss: *Scalarispongia scalaris*; Sfo: *Sarcotragus foetidus*; Sd: *Suberites domuncula*; and Sfi: *Suberites ficus*.

Taxa Per Taxonomic Group	Aa	Da	Fc	Gc	Iv	So	Ss	Sfo	Sd	Sfi
Porifera										
Chondrilla nucula Schmidt, 1862	x									
Chondrosia reniformis Nardo, 1847								x		
Crustacea Amphipoda										
Urothoe sp.	x									
Crustacea Cirripedia										
Acasta sp.	x				x	x	x	x		
Crustacea Decapoda										
Athanas nitescens (Leach, 1814 [in Leach, 1813–1815])	x			x		x	x	x		
Brachyura unid.	x							x		
Dardanus arrosor (Herbst, 1796)		x					x		x	
Decapoda unid.	x							x		
Eualus cranchii (Leach, 1817 [in Leach, 1815–1875])	x							x		
Galathea bolivari Zariquiey Álvarez, 1950	x	x		x	x	x		x		
Galathea intermedia Lilljeborg, 1851	x	x	x		x	x	x	x		
Munida intermedia A. Milne-Edwards & Bouvier, 1899	x									
Munida sp.								x		
Nennalpheus sp.								x		
Pilumnus spinifer H. Milne Edwards, 1833	x	x	x	x	x	x	x	x		x
Pisidia bluteli (Risso, 1816)	x			x						
Synalpheus gambarelloides (Nardo, 1847)		x	x	x	x	x	x	x		
Pagurus prideaux Leach, 1815										x
Crustacea Isopoda										
Carpias stebbingi (Monod, 1933)	x						x	x		
Cymodoce truncata Leach, 1814					x	x	x	x		
Isopoda unid.	x		x							
Mollusca Bivalvia										
Acanthocardia echinata (Linnaeus, 1758)								x		
Aequipecten opercularis (Linnaeus, 1758)			x							
Anadara corbuloides (Monterosato, 1881)			x					x		
Anomia ephippium Linnaeus, 1758								x		
Anomia sp.				x						
Chama gryphoides Linnaeus, 1758								x		
Gregariella semigranata (Reeve, 1858)							x			
Heteranomia squamula (Linnaeus, 1758)								x		
Hiatella arctica (Linnaeus, 1767)	x	x	x	x	x	x	x	x		
Kellia suborbicularis (Montagu, 1803)								x		
Kurtiella bidentata (Montagu, 1803)								x		
Lima lima (Linnaeus, 1758)						x				
Mimachlamys varia (Linnaeus, 1758)	x		x	x			x	x		
Musculus costulatus (Risso, 1826)	x		x		x	x	x	x		
Neopycnodonte cochlear (Poli, 1795)								x		
Pteria hirundo (Linnaeus, 1758)	x									
Striarca lactea (Linnaeus, 1758)					x	x		x		
Veneridae unid.								x		
Mollusca Gastropoda										
Bittium latreillii (Payraudeau, 1826)								x		
Bittium reticulatum (da Costa, 1778)								x		
Calliostoma zizyphinum (Linnaeus, 1758)					x					
Carinorbis clathrata (R. A. Philippi, 1844)								x		
Emarginula multistriata Jeffreys, 1882								x		
Euthria cornea (Linnaeus, 1758)								x		
Fusinus sp.							x			
Hexaplex trunculus (Linnaeus, 1758)								x		
Jujubinus striatus (Linnaeus, 1758)								x		
Cyrillia linearis (Montagu, 1803)								x		
Tritia varicosa (W. Turton, 1825)								x		
Umbraculum umbraculum ([Lightfoot], 1786)	x									
Pseudofusus rostratus (Olivi, 1792)									x	
Cerithriopsis barleei Jeffreys, 1867									x	x
Mollusca Polyplacophora										
Polyplacophora unid.								x		
Polychaeta										
Ceratonereis sp.	x									
Composetia costae (Grube, 1840)								x		
Composetia hircinicola (Eisig, 1869)	x	x	x	x	x	x	x	x		
Eunice sp.	x									

Table 2. *Cont.*

Taxa Per Taxonomic Group	Aa	Da	Fc	Gc	Iv	So	Ss	Sfo	Sd	Sfi
Glyceridae unid.							x	x		
Harmothoe spinifera (Ehlers, 1864)							x			
Harmothoe sp.						x		x		
Scoletoma funchalensis (Kinberg, 1865)								x		
Laetmonice hystrix (Savigny in Lamarck, 1818)								x		
Lepidasthenia elegans (Grube, 1840)	x		x	x			x	x		
Neanthes acuminata (Ehlers, 1868)				x						
Nereididae unid.			x							
Oweniidae unid.				x						
Serpula vermicularis Linnaeus, 1767			x							
Serpulidae unid.						x				
Sternaspis scutata (Ranzani, 1817)								x		
Thelopodidae unid.							x	x		
Sipuncula										
Phascolosoma (Phascolosoma) granulatum Leuckart, 1828	x			x			x	x		
Echinodermata Ophiuroidea										
Amphiura sp.			x							
Ophiothrix fragilis (Abildgaard in O.F. Müller, 1789)	x		x	x		x	x	x		
Ascidiacea										
Didemnidae unid.								x		
Microcosmus vulgaris Heller, 1877			x							
Pyura microcosmus (Savigny, 1816)								x		
Total	25	7	16	14	12	15	20	50	3	4

Mollusks represented the most taxa-rich group (Figure 3), accounting for 42.3% of the total taxa found (33 taxa), followed by crustaceans (25.6%, 20 taxa) and polychaetes (23.1%, 18 taxa). Ascidians accounted for 3.8% (3 taxa), while echinoderms and sponges contributed 2.6% (2 taxa) each to the total taxa pool (Figure 3).

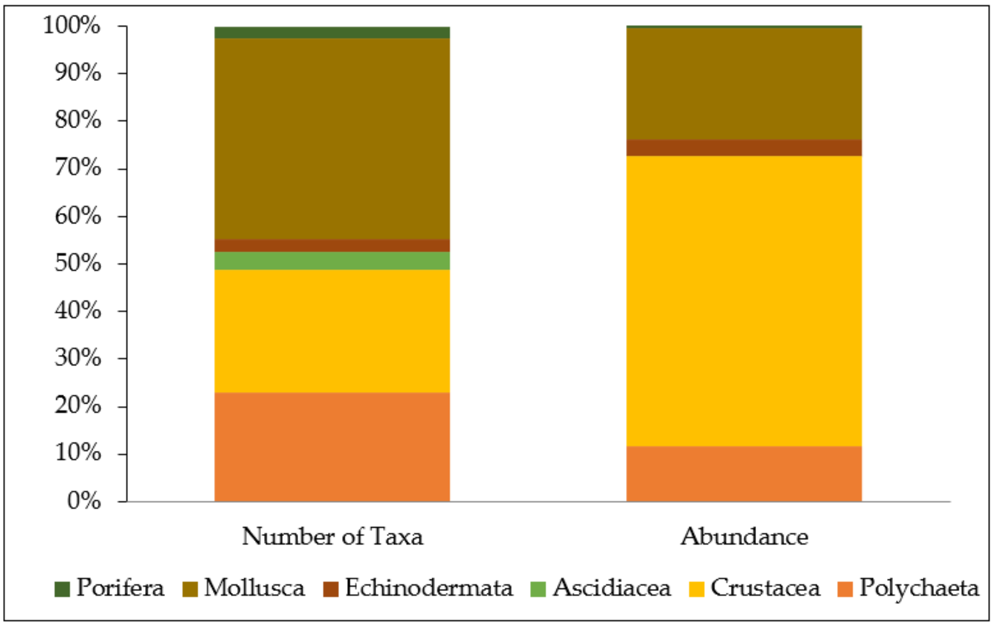

Figure 3. Percentage contribution of each major taxonomic group to the total number of associated taxa (**left**) and total abundance of individuals (**right**), across all sponge specimens examined.

In terms of abundance (Figure 3), crustaceans were the dominant group, comprising 60.8% of all recorded individuals across sponge specimens. They were followed by mollusks (23.6%), polychaetes (11.8%), and echinoderms (3.5%). Ascidians and sponges contributed less than 1% each to the total abundance. At the taxa level, the most abundant associates across all studied sponges were the crustaceans *Synalpheus gambarelloides* and *Dardanus arrosor*, accounting for 30.8% and 16% of the total abundance, respectively, followed by the bivalve *Hiatella arctica* (17.8%).

The most frequently occurring associates were the bivalve mollusk *Hiatella arctica*, found in 57.9% of sponge specimens, the polychaete *Composetia hircinicola* (49.1%), and the decapod crustaceans *Pilumnus spinifer* and *Synalpheus gambarelloides* (44.7% and 36.8%, respectively). All the remaining taxa were recorded in fewer than 17% of the sponge specimens examined.

3.2. Composition of Associated Communities

Mollusks and crustaceans were the only taxonomic groups present in the associated communities of all ten sponge species examined (Figure 4a). Polychaetes were also found in all sponge species except those of the family Suberitidae, while echinoderms were recorded in six of the ten sponge species (they were not found in *Ircinia variabilis*, *Dysidea avara*, and the two species of Suberitidae. Associated ascidians and sponges were found in only two host sponge species: ascidians were associated with *Fasciospongia cavernosa* and *Sarcotragus foetidus*, while sponges were found on *Aplysina aerophoba* and *Sarcotragus foetidus*.

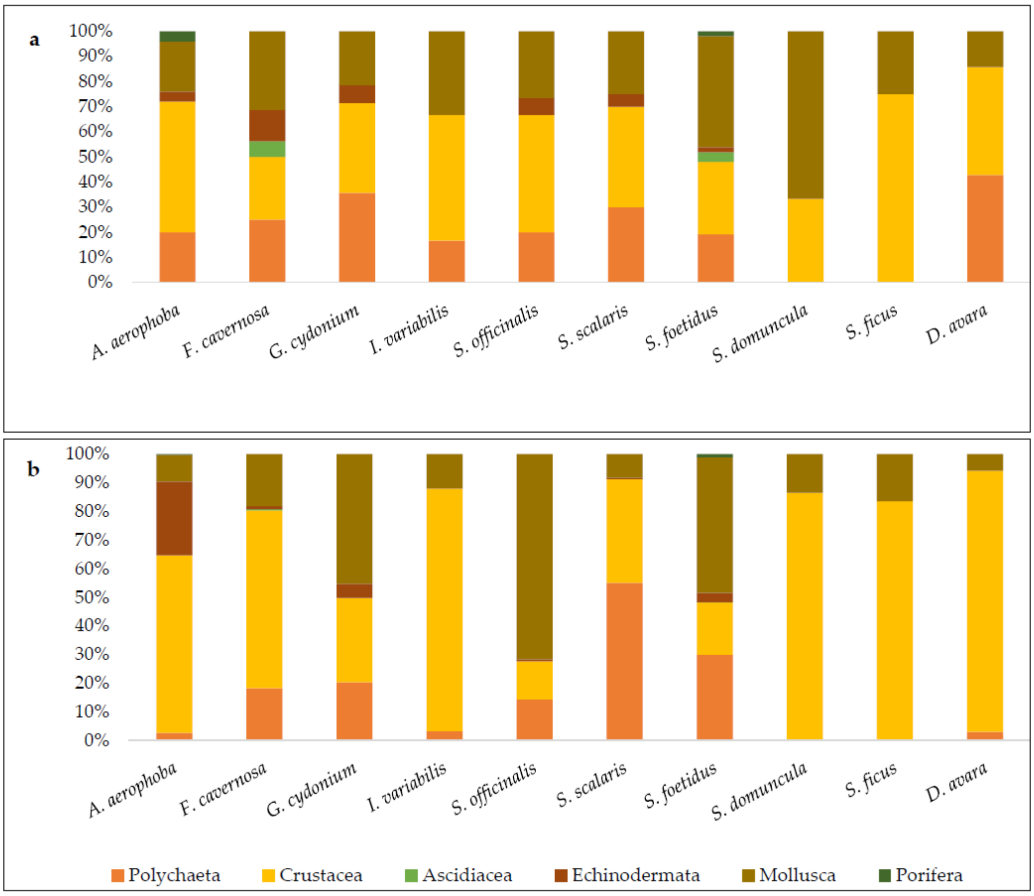

Figure 4. Percentage contribution of higher taxonomic groups to the associated communities of each sponge species in terms of (**a**) number of taxa and (**b**) abundance.

The structure of the associated communities varied across sponge species, particularly in terms of taxa richness within higher taxonomic groups (Figure 4a). Crustaceans and mollusks alternated as the most taxa-rich group among host sponges. Crustaceans exhibited the highest number of taxa in *Aplysina aerophoba* (52%), *Ircinia variabilis* (50%), *Spongia (Spongia) officinalis* (46.7%), *Scalarispongia scalaris* (40%), and *Suberites ficus* (75%), while mollusks dominated in *Fasciospongia cavernosa* (31.3%), *Sarcotragus foetidus* (46%), and *Suberites domuncula* (66.6%). In *Dysidea avara* and *Geodia cydonium*, crustaceans and polychaetes co-dominated, each representing 42.9% and 35.7%, respectively.

In terms of abundance (Figure 4b), crustaceans were the dominant group in six of the ten sponge species: *Aplysina aerophoba* (62%), *Fasciospongia cavernosa* (62.1%), *Ircinia variabilis* (84.6%), *Suberites domuncula* (85.6%), *Suberites ficus* (83.5%), and *Ulosa digitata* (91.3%). Mollusks dominated in *Geodia cydonium* (45.3%), *Spongia (Spongia) officinalis* (71.7%), and *Sarcotragus foetidus* (47.5%), while polychaetes were the dominant group only in *Scalarispongia scalaris*, where they represented 55.1% of total abundance.

Shannon diversity index (H′) and the number of associates per liter of sponge differed significantly among host sponges ($p < 0.05$; Table 3). *Fasciospongia cavernosa* exhibited the highest diversity, followed by *Spongia (Spongia) officinalis*, *Aplysina aerophoba*, *Sarcotragus foetidus*, and *Geodia cydonium*. Intermediate diversity values were observed in *Scalarispongia scalaris*, *Dysidea avara*, and *Ircinia variabilis*, while the lowest values were recorded in *Suberites ficus* and *S. domuncula* (Figure 5). In contrast, Pielou evenness index (J′) did not differ significantly among sponge species (Table 3).

Table 3. Summary of one-way ANOVA results testing the effect of the factor host-sponge on the Shannon diversity index (H′), Pielou species evenness (J′), and the abundance of associates per liter of sponge (N/L). Df: degrees of freedom; *p*: *p*-value. Asterisk (*) denotes statistically significant differences at the 0.05 level.

	Sum of Squares	Df	Mean Square	*p*
Shannon (H′)	19.0263	9	2.11403	0.0000 *
Pielou (J′)	0.461515	8	0.05768	0.0656
N/L	124609	9	13845.5	0.0061 *

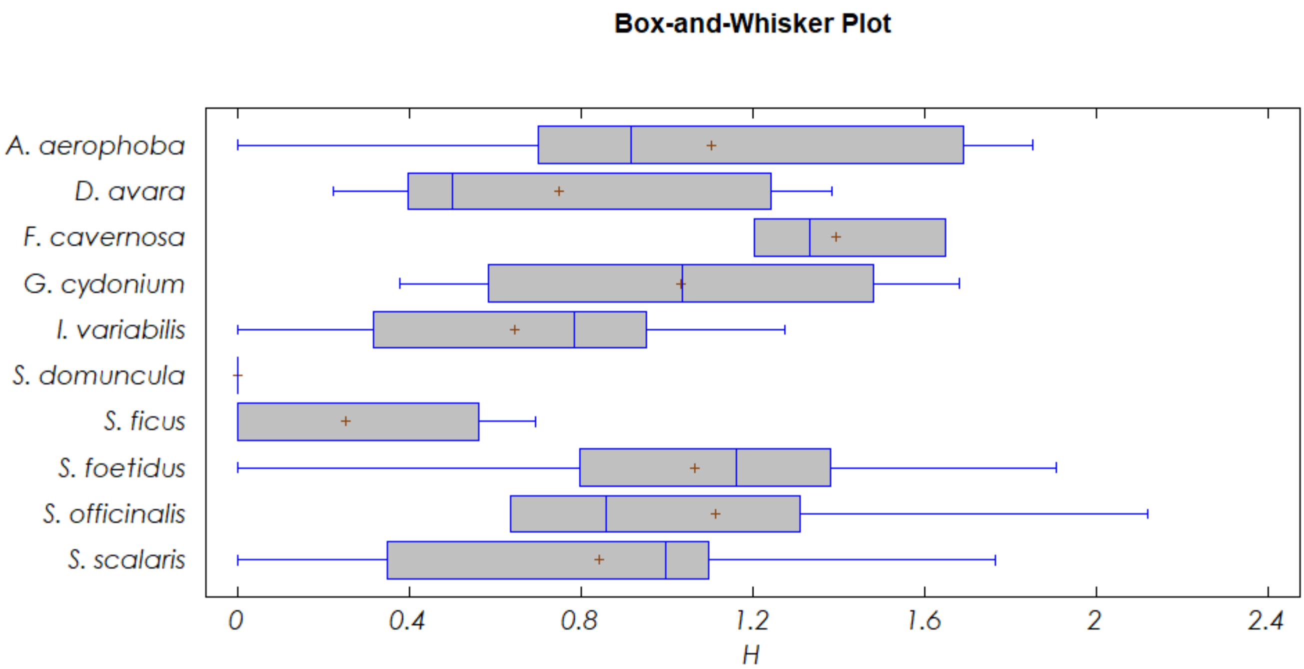

Figure 5. Shannon diversity index (H′) values of the associated communities for each sponge species. Cross (+) denotes the median value.

The composition of the associated communities varied significantly both among the different sponge species and between the two depth zones ($p < 0.05$). Pairwise comparisons among sponge species revealed dissimilarity percentages ranging from 48.64% to 100%, with the highest dissimilarity observed between *Suberites domuncula* and all other sponges (Table 4 and Figure 6).

Table 4. Pairwise dissimilarity (%) in the composition of associated communities among the examined sponge species. Aa: *Aplysina aerophoba*; Da: *Dysidea avara*; Fc: *Fasciospongia cavernosa*; Gc: *Geodia cydonium*; Iv: *Ircinia variabilis*; So: *Spongia (Spongia) officinalis*; Ss: *Scalarispongia scalaris*; Sfo: *Sarcotragus foetidus*; Sd: *Suberites domuncula*; and Sfi: *Suberites ficus*.

	SFo	Fc	Ss	Iv	Da	So	Sd	SFi	Aa
Gc	68.84	75.47	72.01	77.44	77.82	62.44	100.00	96.00	88.51
Aa	90.64	88.14	91.97	94.63	89.60	88.25	100.00	96.34	
SFi	95.38	96.86	98.05	97.92	94.07	95.67	97.77		
Sd	100.00	100.00	99.47	100.00	96.09	100.00			
So	62.76	70.50	61.50	74.45	71.72				
Da	69.35	50.31	77.50	48.64					
Iv	73.69	57.93	77.19						
Ss	66.13	71.96							
Fc	68.01								

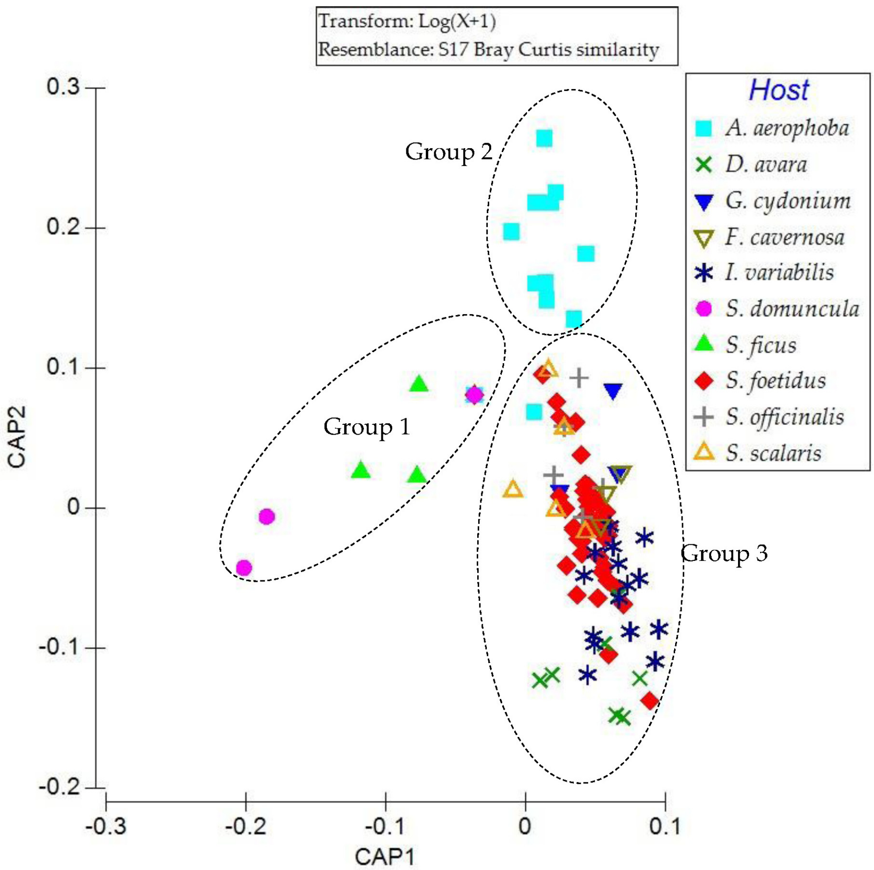

Figure 6. Canonical Analysis of Principal Coordinates (CAP) plot for the associated communities of each sponge species (host), based on abundance data.

The examined sponge specimens appeared to group into three distinct clusters, based on the composition of their associated fauna (Figure 6). The sponges of the order Suberitida, characterized by monospecific associated communities, formed a clearly separated cluster (Group 1), with dissimilarity exceeding 94%. The specimens of *Aplysina aerophoba*, representing the order Verongiida, also formed a distinct cluster (Group 2), with dissimilarity percentages greater than 88% from all other species. A third, more heterogeneous cluster (Group 3) included species of the order Dictyoceratida, along with *Geodia cydonium* which belongs to the order Tetractinellida.

SIMPER analysis revealed that dissimilarity between the associated communities of Group 2 (*Aplysina aerophoba* specimens) (Appendix A Table A2) and those of Group 3 (Dictyoceratida and *Geodia cydonium*) (Appendix A Tables A3–A9) was primarily due to the absence of three taxa from Group 2 specimens, which were present in high abundances in almost all specimens of Group 3. These associates were the bivalve *Hiatella arctica*, the decapod *Synalpheus gambarelloides*, and the polychaete *Composetia hirsinicola*. On the other hand, the associated communities of Group 2 were characterized by high abundance of the decapod *Galathea intermedia* and the brittle star *Ophiothrix fragilis*, neither of which was recorded in Group 3 specimens.

Different associated taxa dominated in each of the host sponges examined, as presented in detail in the Appendix A. The decapod *Synalpheus gambarelloides* dominated in terms of abundance, accounting for more than 50% in three sponge species: *Dysidea avara* (Appendix A, Table A3), *Fasciospongia cavernosa* (Appendix A, Table A4), and *Ircinia variabilis* (Appendix A, Table A5). The bivalve *Hiatella arctica* was dominant in the associated communities of *Spongia (Spongia) officinalis* (Appendix A, Table A6), *Geodia cydonium* (Appendix A, Table A7), and *Sarcotragus foetidus* (Appendix A, Table A8), representing nearly 70% of total abundance in the first species and more than 40% in the other two. In the sponge *Scalarispongia scalaris*, the polychaete *Composetia hirsinicola* was the most abundant associated taxa (Appendix A Table A9).

The highest taxa-per-liter ratio (S/L) of associated fauna was recorded in the sponge *Suberites domuncula* (S/L = 13.39), followed by *Fasciospongia cavernosa* (8.38), *Dysidea avara* (7.07), *Suberites ficus* (6.15), *Aplysina aerophoba* (5.91) and *Spongia (Spongia) officinalis* (5.70). All the remaining sponge species had S/L values below 3.5. Notably, although *Sarcotragus foetidus* hosted the highest number of associates, it exhibited the lowest taxa-per-liter ratio (S/L = 0.84).

Correlation analyses between sponge volume and community parameters (i.e., associated taxa richness, abundance, and Shannon diversity index) revealed positive relationships for all sponge species except *Fasciospongia cavernosa* and *Dysidea avara* (Table 5). In the former sponge volume was negatively correlated with all the above parameters, while in the latter sponge volume was negatively correlated with Shannon diversity index. For *Suberites domuncula*, correlation with the number of associates or Shannon diversity index was not applicable, since each specimen hosted one single associated taxon.

Table 5. Spearman's rank correlation coefficient between sponge volume and taxa richness (S), abundance (N) and Shannon diversity index (H').

	S	N	H'
Aplysina aerophoba	0.731	0.513	0.797
Dysidea avara	0.132	0.546	−0.043
Fasciospongia cavernosa	−0.139	−0.417	−0.688
Geodia cydonium	0.909	0.856	0.877
Ircinia variabilis	0.463	0.131	0.513
Sarcotragus foetidus	0.718	0.791	0.316
Spongia (Spongia) officinalis	0.497	0.128	0.865
Scalarispongia scalaris	0.509	0.673	0.584
Suberites domuncula		0.924	
Suberites ficus	0.744	0.267	0.825

3.3. Effect of Subarea and Depth on Sponge-Associated Communities

As indicated by the PERMANOVA results for each sponge species (Table 6), the geographic range of the sampling area did not significantly influence the composition of the associated communities for most species, with the exception of *Sarcotragus foetidus* and *Suberites domuncula* (Table 6).

Table 6. Statistical significance value (*p*-value) of the factor subarea in the composition of the associated community of each sponge species. Df: degrees of freedom. Asterisk (*) indicates statistically significant differences at the 0.001 level.

	Sum of Squares	Df	Mean Square	*p*
Aplysina aerophoba	7242	2	3621	0.306
Dysidea avara	2261.6	2	1130.8	0.318
Fasciospongia cavernosa	1561.6	1	1561.6	0.662
Geodia cydonium	5203.3	2	2601.6	0.172
Ircinia variabilis	—	—	—	—
Sarcotragus foetidus	8410	2	4205	0.009 *
Spongia (Spongia) officinalis	4894.6	2	2447.3	0.399
Scalarispongia scalaris	2600.6	1	2600.6	0.323
Suberites domuncula	19443	1	19443	0.002 *
Suberites ficus	1786.3	1	1786.3	0.720

As described in Section 2, the effect of depth on sponge-associated communities was investigated for the species *Sarcotragus foetidus* and *Aplysina aerophoba*, of which sufficient specimens were available from both depth zones (20–50 and 50–200 m).

The influence of depth varied among all parameters examined (Table 7). For *Aplysina aerophoba*, depth did not appear to have a statistically significant effect on any of the examined parameters (Shannon diversity index, Pielou evenness index, number of taxa, and abundance of associates per liter of sponge). In contrast, depth significantly influenced the abundance of associates in the community of *Sarcotragus foetidus*, with lower abundance recorded at 50–200 m compared to the 20–50 m depth zone. However, diversity and evenness indices were not significantly affected by depth.

Table 7. Summary of one-way ANOVA results for the two examined depth zones (20–50 m and 50–200 m) for the following community parameters: Shannon diversity index (H′); Pielou species evenness (J′), taxa richness (S) and associates' abundance per liter of sponge (N/L). Df: degrees of freedom; *p*: *p*-value. Asterisk (*) indicates statistically significant differences at the 0.05 level.

	Sum of Squares	Df	Mean Square	*p*
Sarcotragus foetidus				
Shannon (H′)	0.387686	1	0.387686	0.1822
Pielou (J′)	0.0193038	1	0.0193038	0.3858
N/L	25,181.9	1	25,181.9	0.0008 *
S	48.4455	1	48.4455	0.0569
Aplysina aerophoba				
Shannon (H′)	0.14279	1	0.14279	0.5402
Pielou (J′)	0.018930	1	0.018930	0.3290
N/L	17,710.1	1	17,710.1	0.0627
S	0	1	0	1.0000

4. Discussion

Sponges are widely recognized as important habitat formers in various types of benthic habitats globally [1], and more specifically in the Mediterranean Sea (e.g., [5,6,12,16,20]). Understanding the ecology and structure of sponge-associated communities is crucial, as it enhances our knowledge of how these organisms contribute to the overall diversity and abundance of benthic ecosystems. This is particularly important for regions as the eastern Mediterranean, where ecological data from mesophotic and deep soft-substrate habitats remain limited. Despite its oligotrophic nature, this region has historically supported rich commercial sponge grounds in the Mediterranean basin [21,22]. Moreover, recent research has documented diverse sponge assemblages from bottom trawling grounds in the Aegean and Ionian Seas [10], further highlighting the ecological significance of these often-overlooked habitats.

The findings of this study—documenting 78 macrofaunal taxa and over 4600 individuals associated with ten sponge species—demonstrate that sponges significantly contribute to local biodiversity and structural complexity, even in trawled soft-substrate environments.

Among the associated taxa, mollusks and crustaceans alternated in dominance in terms of both taxa richness and abundance, while polychaetes consistently ranked third for both parameters. This pattern aligns with previous observations of sponge-associated communities in the eastern Mediterranean, reported for both hard [5,11,15,23,24] and soft substrates [18], as well as with studies conducted in tropical ecosystems [25].

Crustaceans have been found as the most abundant group in shallow sponge-associated communities [12,13,15,16] and in cave-dwelling sponges in the Aegean Sea [5]. The decapod *Synalpheus gambarelloides*, a sponge-dwelling snapping shrimp, was the most abundant crustacean in this study, dominating the associated communities in three sponge species (*Dysidea avara*, *Fasciospongia cavernosa*, and *Ircinia variabilis*). This pattern is consistent with previous studies from the Aegean and Levantine Seas [16,18,26]. Its dominance can be attributed to the social behavior and cooperative defense strategies typical of *Synalpheus* species, which are obligate sponge symbionts [27,28], as well as to their small size and high mobility that make them successful symbionts. Furthermore, the high occurrence of these snapping shrimps in these particular sponges appears to be associated with the large and spacious canals provided, which facilitate shrimp settlement. Notably, when shrimps inhabit sponges with narrower cavities and canals, such as those of *Sarcotragus foetidus*, they have been observed to enlarge the canals to a preferred size by consuming sponge tissue [16].

Among bivalve mollusks, *Hiatella arctica* was the most abundant, forming dense populations in *Geodia cydonium* and *Sarcotragus foetidus*. This bivalve has been frequently reported as a member of sponge-associated communities [5,12,29], preferring sponges with spacious canals and internal cavities [12], as observed in our study. Interestingly, while *Hiatella arctica* individuals are often covered with host sponge tissue [12], this was not observed in our samples, except in cases of empty, non-living shells. All living bivalves found in our study were freely located within the cavities of the sponges.

The brittle star *Ophiothrix fragilis* was the only echinoderm encountered. This species has been commonly documented as a sponge epibiont [5,11,12] mainly in sponges with pronounced surface relief and cavities, such as *Agelas oroides* and *Aplysina aerophoba* [12]. In our study, *O. fragilis* was also primarily found inhabiting the surface cavities of *A. aerophoba*, supporting previous findings.

While a relatively rare phenomenon [15,30,31], epibiotic sponges were also observed. In this study, two sponge species typical of hard substrates, *Chondrilla nucula* and *Chondrosia reniformis*, were found as epibionts on the surface of *Aplysina aerophoba* and *Sarcotragus foetidus* specimens. This finding supports the important role of sponges as habitat formers in soft bottoms, serving as "hard substrate islands" in extended soft sedimentary areas, thus offering settlement opportunities for species that typically inhabit hard substrates.

The composition of sponge-associated communities varied among host species. The greatest differentiation was observed between the faunal community associated with *Aplysina aerophoba* and those of the two examined *Suberites* species (*S. domuncula* and *S. ficus*). These sponges have very different morphology and structural features: *Aplysina aerophoba* typically has digitate projections with compact texture and few large canals—usually only one central canal per projection—while *Suberites* species have a dense, nearly spherical structure with a single central cavity. The external morphology of *A. aerophoba*, with its prominent surface cavities, favors colonization by larger and motile epibionts, such as the brittle star *Ophiothrix fragilis* and the anomuran decapod *Galathea intermedia*. Similar preferences have been reported in previous studies [12], where *O. fragilis* was found to prefer host sponges with strong surface relief and invaginations, like *A. aerophoba*.

Moreover, the associated communities of the examined sponges of the order Dictyoceratida, along with *Geodia cydonium*, exhibited similarities in species composition. These sponges are generally characterized by massive shapes and spacious, dense, and complex canal systems. Their associated communities were dominated by decapods (e.g., *Synalpheus gambarelloides*, *Athanas nitescens*), bivalves (*Hiatella arctica*), and polychaetes (*Composetia hirsinicola*), which is consistent with similar observations from sponges on soft substrates in the Levantine Sea [18]. These findings, coupled with the lack of statistically significant differences between the associated communities of the same sponge species across different sampling areas, further support the idea that sponge morphology is the primary factor influencing the composition of their associated communities [12]. This pattern does not appear to be restricted to the Mediterranean, as similar trends have been observed in amphipod populations associated with Dictyoceratida sponges from tropical regions [32].

Depth did not significantly affect Shannon diversity (H′), evenness, or taxa richness for the associated community of the two sponge species examined across depth gradients (*A. aerophoba* and *S. foetidus*), in line with similar findings from the Israeli coast [17]. However, *S. foetidus* specimens from the deeper zone (50–200 m) harbored significantly fewer individuals, echoing the general trend of declining faunal abundance with increasing depth [33–36]. Nevertheless, this depth-related variability requires further investigation to better understand its impact on sponge-associated communities.

Overall, the results of this study highlight the essential ecological role of sponges as habitat formers on mesophotic soft-substrate bottoms. Sponges provide refuge for diverse endobiotic invertebrates and function as "islands" of stable substrate within extensive muddy or sandy seafloors, on which sessile epibionts (e.g., other sponges, ascidians, and bryozoans), can settle. With this role, sponges enhance habitat complexity and benthic diversity in environments frequently disturbed by bottom-towed fishing gear. This becomes crucial in environments with limited sponge abundance, such as muddy bottoms, as it has been observed that in areas with low sponge diversity all available symbionts settle on the few sponges that are present [16]. Thus, the few available sponges accommodate disproportionately greater diversity, providing essential shelter and establishment opportunities for the associated organisms. Consequently, their removal during fishing operations not only causes direct mortality of the sponges themselves, but also destroys the complex communities they support.

In conclusion, this study highlights the need for comprehensive assessments of the functional role of sponges in the Mediterranean Sea and beyond. We also recommend that sponge-associated communities should be explicitly considered as part of the discards in trawl fisheries, since this type of fishing removes entire sections of host sponges and the diverse fauna they sustain.

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Appendix A

Table A1. List of specimens per sponge species and information on the depth zone of collection, wet weight, volume, number of associated taxa (S) and number of individuals (N) found in each sample.

	Depth Zone (m)	Wet Weight (gr)	Volume (mL)	S	N
Aplysina aerophoba					
#2	50–200	771.3	510	9	73
#3	50–200	781	600	9	107
#4	50–200	307	152	3	17
#5	50–200	369	200	6	29
#8	20–50	670	640	6	11
#38	20–50	305	180	2	3
#58	20–50	1050	980	8	35
#109	50–200	312	250	2	2
#122	50–200	68	45	1	1
#147	20–50	237	250	3	9
#148	20–50	275	240	7	22
#162	20–50	207	180	3	7
Dysidea avara					
#47	20–50	232	250	3	27
#130	20–50	218	230	3	29
#139	20–50	195	200	4	11
#140	20–50	75	90	2	5
#166	50–200	172	20	2	17
#189	20–50	161	130	4	12
#228	20–50	65	70	5	17
Fasciospongia cavernosa					
#34	20–50	594	480	10	74
#35	20–50	714	980	8	35
#59	20–50	445	450	7	33
Geodia cydonium					
#1	20–50	13,100	6720	12	166
#97	20–50	1949	1760	4	46
#197	20–50	2840	3900	4	24
#214	20–50	2082	2480	2	8

Table A1. *Cont.*

	Depth Zone (m)	Wet Weight (gr)	Volume (mL)	S	N
Ircinia variabilis					
#17	20–50	253	230	4	31
#19	20–50	194.5	180	3	32
#49	50–200	1926	1770	3	10
#136	20–50	310	340	3	27
#137	20–50	512	500	4	75
#149	20–50	235	290	4	41
#150	20–50	154	190	3	20
#151	20–50	66.5	70	1	11
#152	20–50	50	25	2	8
#153	20–50	50	25	1	6
#154	20–50	86	50	1	2
#168	20–50	378	380	4	40
#178	50–200	999	950	4	9
#304	50–200	1781	1790	4	8
#306	20–50	961	1130	3	118
Sarcotragus foetidus					
#11	20–50	73	30	2	7
#12	20–50	281.3	275	3	40
#13	20–50	2588.6	2120	9	247
#28	50–200	877	890	6	59
#29	20–50	768	795	3	61
#33	20–50	3578	3120	8	104
#37	20–50	2120	2010	8	165
#39	50–200	840	750	6	17
#43	20–50	1635	1500	6	95
#64	20–50	770	680	11	92
#77	50–200	2350	2180	8	34
#78	50–200	2223	2210	5	76
#94	20–50	517	450	6	26
#95	20–50	440	350	6	39
#96	20–50	325	225	4	9
#113	20–50	7325	7200	16	611
#115	50–200	706	870	8	77
#116	50–200	304	300	4	12
#117	50–200	228	260	2	3
#131	50–200	222	240	1	1
#142	20–50	432.4	400	5	22
#143	20–50	269	305	4	14
#155	20–50	1923	2210	10	280
#156	50–200	1771	2610	6	21
#167	20–50	662	670	12	103
#176	50–200	1236	1050	6	42
#177	50–200	1239	1150	6	30
#179	50–200	3510	4045	12	63
#183	20–50	6608	6450	16	304
#184	50–200	851	950	5	30
#190	20–50	459.2	500	5	33
#195	20–50	1503	1500	11	49
#196	50–200	2920	3030	4	57
#210	50–200	109.5	80	4	9
#211	50–200	393.4	400	1	4
#212	50–200	474.8	450	1	1
#226	20–50	535	640	2	18
#230	20–50	461	470	4	23
#233	20–50	2300	2300	7	86
#305	50–200	1168	1710	3	11
Scalarispongia scalaris					
#7	20–50	2678	2560	12	162
#14	50–200	2060	1900	2	9
#36	20–50	780	650	8	35
#48	50–200	665	630	7	64
#69	50–200	30	15	1	1
Spongia (Spongia) officinalis					
#25	50–200	1150	1090	4	15
#118	50–200	92	100	2	3
#165	20–50	1173	1100	11	31
#169	20–50	205.6	90	6	43
#208	20–50	182.5	250	2	6
Suberites domuncula					
#70	50–200	48	35	1	3
#110	50–200	22	20	1	1
#111	50–200	21	20	1	2
#264	20–50	10	10	1	1
#300	20–50	10	10	1	1
#301	20–50	12	10	1	1
#302	20–50	10	10	1	1

Table A1. *Cont.*

	Depth Zone (m)	Wet Weight (gr)	Volume (mL)	S	N
#303	20–50	10	10	1	1
#304	20–50	11	10	1	1
#305	20–50	10	10	1	1
#306	20–50	10	10	1	1
#307	20–50	12	11	1	1
#308	20–50	10	10	1	1
#309	20–50	11	10	1	1
#310	20–50	10	10	1	1
#311	20–50	9	8	1	1
#312	20–50	10	10	1	1
#313	20–50	10	10	1	1
Suberites ficus					
#107	50–200	494	425	2	2
#108	50–200	101	110	2	4
#290	50–200	70	60	1	1
#555	50–200	10	10	1	1
#556	50–200	50	45	1	1

Table A2. List of taxa comprising the community associated with the sponge *Aplysina aerophoba*. P: presence; F: frequency of appearance; mDa: mean dominant abundance (%); and cDa: cumulative abundance (%).

	P	F	mDa	cDa
Ophiothrix fragilis	7	58.3	25.8	25.8
Galathea intermedia	7	58.3	24.6	50.4
Galathea bolivari	4	33.3	15.6	65.9
Pisidia bluteli	4	33.3	6.0	72.0
Carpias stebbingi	3	25.0	4.5	76.4
Hiatella arctica	3	25.0	4.4	80.8
Athanas nitescens	2	16.7	3.8	84.6
Musculus costulatus	3	25.0	3.6	88.2
Pilumnus spinifer	5	41.7	2.7	90.9
Eualus cranchii	3	25.0	1.5	92.4
Urothoe sp.	2	16.7	1.4	93.8
Ceratonereis sp.	1	8.3	1.1	94.9
Lepidasthenia elegans	1	8.3	0.9	95.8
Mimachlamys varia	1	8.3	0.9	96.6
Munida intermedia	1	8.3	0.6	97.2
Isopoda unid.	1	8.3	0.5	97.7
Umbraculum umbraculum	1	8.3	0.4	98.1
Brachyura unid.	1	8.3	0.3	98.5
Eunice sp.	1	8.3	0.3	98.8
Decapoda unid.	1	8.3	0.3	99.1
Acasta sp.	1	8.3	0.2	99.3
Pteria hirundo	1	8.3	0.2	99.5
Phascolosoma (Phascolosoma) granulatum	1	8.3	0.2	99.7
Chondrilla nucula	1	8.3	0.2	99.8
Composetia hircinicola	1	8.3	0.2	100

Table A3. List of taxa comprising the community associated of the sponge *Dysidea avara*. P: presence; F: frequency of appearance; mDa: mean dominant abundance (%); and cDa: cumulative abundance (%).

	P	F	mDa	cDa
Synalpheus gambarelloides	7	100.0	81.5	81.5
Hiatella arctica	5	71.4	5.8	87.3
Pilumnus spinifer	5	71.4	5.3	92.6
Composetia hircinicola	3	42.9	2.9	95.5
Dardanus arrosor	1	14.3	2.8	98.3
Galathea intermedia	1	14.3	1.0	99.3
Galathea bolivari	1	14.3	0.7	100.0

Table A4. List of taxa comprising the community associated of the sponge *Fasciospongia cavernosa*. P: presence; F: frequency of appearance; mDa: mean dominant abundance (%); and cDa: cumulative abundance (%).

	P	**F**	**mDa**	**cDa**
Synalpheus gambarelloides	3	100.0	51.4	51.4
Composetia hircinicola	2	66.7	15.5	66.9
Hiatella arctica	3	100.0	12.3	79.2
Galathea intermedia	1	33.3	5.5	84.8
Pilumnus spinifer	2	66.7	3.6	88.3
Anadara corbuloides	2	66.7	2.5	90.8
Musculus costulatus	2	66.7	1.6	92.4
Isopoda unid.	1	33.3	1.6	94.0
Serpula vermicularis	2	66.7	1.2	95.2
Aequipecten opercularis	1	33.3	0.8	96.0
Lepidasthenia elegans	1	33.3	0.8	96.9
Amphiura sp.	1	33.3	0.8	97.7
Mimachlamys varia	1	33.3	0.8	98.4
Nereididae unid.	1	33.3	0.8	99.2
Microcosmus vulgaris	1	33.3	0.4	99.6
Ophiothrix fragilis	1	33.3	0.4	100.0

Table A5. List of taxa comprising the community associated of the sponge *Ircinia variabilis*. P: presence; F: frequency of appearance; mDa: mean dominant abundance (%); and cDa: cumulative abundance (%).

	P	**F**	**mDa**	**cDa**
Synalpheus gambarelloides	12	80.0	78.9	78.9
Hiatella arctica	10	66.7	11.4	90.3
Composetia hircinicola	7	46.7	3.1	93.3
Acasta sp.	2	13.3	2.3	97.8
Cymodoce truncata	1	6.7	0.6	98.4
Pilumnus spinifer	4	26.7	0.5	99.0
Galathea intermedia	1	6.7	0.3	99.3
Striarca lactea	1	6.7	0.2	99.6
Thelopodidae unid.	2	13.3	0.2	99.7
Galathea bolivari	1	6.7	0.1	99.9
Musculus costulatus	1	6.7	0.1	100.0
Calliostoma zizyphinum	1	6.7	0.0	100.0

Table A6. List of taxa comprising the community associated of the sponge *Spongia (Spongia) officinalis*. P: presence; F: frequency of appearance; mDa: mean dominant abundance (%); and cDa: cumulative abundance (%).

	P	**F**	**mDa**	**cDa**
Hiatella arctica	5	100	70.1	70.1
Composetia hircinicola	3	60	14	84.2
Acasta sp.	2	40	5.6	89.8
Pilumnus spinifer	3	60	2.7	92.5
Cymodoce truncata	1	20	1.9	94.4
Galathea bolivari	1	20	1.9	96.4
Athanas nitescens	1	20	0.8	97.2
Lima lima	1	20	0.8	97.9
Musculus costulatus	1	20	0.6	98.6
Ophiothrix fragilis	1	20	0.6	99.2
Galathea intermedia	1	20	0.2	99.4
Harmothoe unid.	1	20	0.2	99.5
Serpulidae unid.	1	20	0.2	99.7
Striarca lactea	1	20	0.2	99.8
Synalpheus gambarelloides	1	20	0.2	100.0

Table A7. List of taxa comprising the community associated of the sponge *Geodia cydonium*. P: presence; F: frequency of appearance; mDa: mean dominant abundance (%); and cDa: cumulative abundance (%).

	P	**F**	**mDa**	**cDa**
Geodia cydonium				
Hiatella arctica	4	100.0	41.8	41.8
Athanas nitescens	1	25.0	19.5	61.4
Composetia hircinicola	3	75.0	17.5	78.9
Pilumnus spinifer	2	50.0	5.0	83.8
Ophiothrix fragilis	2	50.0	4.3	88.1
Pisidia bluteli	1	25.0	4.2	92.3
Anomia sp.	1	25.0	2.8	95.2
Neanthes acuminata	1	25.0	1.2	96.4
Lepidasthenia elegans	1	25.0	0.9	97.4
Mimachlamys varia	2	50.0	0.9	98.3
Galathea bolivari	1	25.0	0.7	99.0
Phascolosoma (Phascolosoma) granulatum	1	25.0	0.5	99.5
Oweniidae unid.	1	25.0	0.2	99.8
Synalpheus gambarelloides	1	25.0	0.2	100.0

Table A8. List of taxa comprising the community associated of the sponge *Sarcotragus foetidus*. P: presence; F: frequency of appearance; mDa: mean dominant abundance (%); and cDa: cumulative abundance (%).

	P	**F**	**mDa**	**cDa**
Hiatella arctica	33	82.5	38.4	38.4
Composetia hircinicola	31	77.5	24.3	62.7
Synalpheus gambarelloides	16	40.0	9.1	71.8
Striarca lactea	15	37.5	7.1	78.9
Pilumnus spinifer	26	65.0	4.5	83.4
Ophiothrix fragilis	4	10.0	3.2	86.6
Cymodoce truncata	6	15.0	2.5	89.1
Lepidasthenia elegans	15	37.5	1.7	90.8
Phascolosoma (Phascolosoma) granulatum	8	20.0	1.3	92.1
Composetia costae	3	7.5	1.0	94.2
Scoletoma funchalensis	10	25.0	0.8	94.9
Thelopodidae unid.	10	25.0	0.8	95.7
Acasta sp.	2	5	0.7	96.4
Galathea intermedia	6	15.0	0.5	96.9
Emarginula multistriata	1	2.5	0.4	97.3
Mimachlamys varia	5	12.5	0.3	97.6
Anadara corbuloides	1	2.5	0.3	97.9
Neopycnodonte cochlear	2	5.0	0.3	98.2
Athanas nitescens	5	12.5	0.3	98.4
Musculus costulatus	2	5.0	0.2	98.6
Nennalpheus sp.	2	5.0	0.2	98.8
Decapoda unid.	3	7.5	0.1	98.9
Galathea bolivari	1	2.5	0.1	99.1
Polyplacophora unid.	1	2.5	0.1	99.1
Brachyura unid.	3	7.5	0.1	99.2
Glyceridae unid.	2	5.0	0.1	99.3
Bittium reticulatum	2	5.0	0.1	99.3
Kurtiella bidentata	1	2.5	0.1	99.4
Carpias stebbingi	2	5.0	0.1	99.5
Chama gryphoides	1	2.5	0.1	99.5
Heteranomia squamula	1	2.5	0.1	99.6
Pyura microcosmus	1	2.5	0.1	99.6
Sternaspis scutata	1	2.5	0.1	99.7
Eualus cranchii	2	5.0	0.1	99.8
Carinorbis clathrata	1	2.5	0.0	99.8
Harmothoe sp.	1	2.5	0.0	99.8
Didemnidae unid.	1	2.5	0.0	99.9
Laetmonice hystrix	2	5.0	0.0	99.9
Munida sp.	1	2.5	0.0	99.9
Euthria cornea	1	2.5	0.0	99.9
Veneridae unid.	1	2.5	0.0	99.9
Anomia ephippium	1	2.5	0.0	99.9
Cyrillia linearis	1	2.5	0.0	100.0
Kellia suborbicularis	1	2.5	0.0	100.0
Jujubinus striatus	1	2.5	0.0	100.0
Acanthocardia echinata	1	2.5	0.0	100.0
Bittium latreillii	1	2.5	0.0	100.0
Hexaplex trunculus	1	2.5	0.0	100.0
Tritia pygmaea	1	2.5	0.0	100.0

Table A9. List of taxa comprising the community associated of the sponge *Scalarispongia scalaris*. P: presence; F: frequency of appearance; mDa: mean dominant abundance (%); and cDa: cumulative abundance (%).

	P	F	mDa	cDa
Composetia hircinicola	5	100	53.1	53.1
Acasta sp.	2	40	28.0	81.1
Hiatella arctica	3	60	6.9	88.0
Carpias stebbingi	1	20	2.6	90.5
Cymodoce truncata	1	20	1.5	92.0
Pilumnus spinifer	2	40	1.3	93.4
Galathea intermedia	1	20	1.1	94.4
Synalpheus gambarelloides	2	40	1.1	95.5
Lepidasthenia elegans	1	20	0.5	96.0
Musculus costulatus	1	20	0.5	96.6
Ophiothrix fragilis	1	20	0.5	97.1
Thelopodidae unid.	1	20	0.5	97.7
Athanas nitescens	1	20	0.5	98.2
Fusinus sp.	1	20	0.5	98.7
Harmothoe spinifera	1	20	0.5	99.3
Glyceridae unid.	1	20	0.2	99.5
Dardanus arrosor	1	20	0.1	99.6
Gregariella semigranata	1	20	0.1	99.7
Mimachlamys varia	1	20	0.1	99.9
Phascolosoma (Phascolosoma) granulatum	1	20	0.1	100.0

Table A10. List of taxa comprising the community associated of the sponge *Suberites domuncula*. P: presence; F: frequency of appearance; mDa: mean dominant abundance (%); and cDa: cumulative abundance (%).

	P	F	mDa	cDa
Dardanus arrosor	15	83.3	86.5	86.5
Cerithiopsis barleei	2	11.1	10.6	97.1
Gracilipurpura rostrata	1	5.6	2.9	100.0

Table A11. List of taxa comprising the community associated of the sponge *Suberites ficus*. P: presence; F: frequency of appearance; mDa: mean dominant abundance (%); and cDa: cumulative abundance (%).

	P	F	mDa	cDa
Pagurus prideaux	2	40	67.9	67.9
Cerithiopsis barleei	2	40	16.5	84.4
Paguridae unid.	1	20	9.3	93.6
Pilumnus spinifer	2	40	6.4	100.0

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