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Sponge Community Patterns in Mesophotic and Deep-Sea Habitats in the Aegean and Ionian Seas

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Abstract: Sponge assemblages play a significant role in the functioning of the Mediterranean benthic ecosystem. The main goal of this study was to investigate the diversity and distribution of poorly known sponge communities in the mesophotic and deep-sea substrates of the eastern Mediterranean Sea. More than 1500 sponge specimens belonging to 87 taxa were collected from 156 stations during experimental and commercial bottom trawling in the Aegean Sea and the eastern part of the Ionian ecoregion, at depths of between 10 and 800 m. A total of 79 sponge species were found in the Aegean and 40 species in the Ionian Sea. Eight of these species are included in lists of endangered and threatened species, two were newly recorded in the Aegean and six were first recorded in the east Ionian Sea. Both community structure and diversity differed between the two ecoregions. Species richness, biomass, abundance and diversity decreased with increasing depth, while different species dominated, in terms of biomass, abundance and frequency of appearance, in the two ecoregions and the separate depth zones. In contrast with previous investigations, which mostly examined shallow-water sponges, no clear resemblance patterns were observed among the north and south Aegean subareas, probably due to the homogeneity of the deep-sea habitats under investigation. This study, using sampling material from fish stock monitoring programs for the first time, contributed to our knowledge of the largely unknown eastern Mediterranean mesophotic and deep-sea sponge populations, which are subjected to intensive trawling activities.

Keywords: Porifera; benthos; MEDITS; dark habitats; eastern Mediterranean

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1. Introduction

Within the marine realm, most of our current knowledge comes from the investigation of shallow coastal habitats and depths that can be easily reached with various sampling techniques (i.e., 0–30 m). Our knowledge of the mesophotic (30–200 m) and deep-sea habitats (>200 m) is limited and generally linked to the development of new technologies and sampling techniques [1].

In the literature, the 30–150 m bathymetric range is frequently used to delimit the mesophotic zone [2]. Usually, the lowest boundary corresponds to the deepest occurrence of zooxanthellate corals but varies at a global scale. In the Mediterranean Sea, which is a mid-latitude, semi-enclosed and oligotrophic basin, the depth corresponding to the lower mesophotic limit varies from almost 150 m in the western basin to almost 200 m in the Aegean and the Levantine Seas [2].

The deep sea, typically the waters deeper than 200 m [3], is the world's largest habitat, as it encompasses more than 65% of the planet's surface [4], and the least explored environment [5]. Despite the enormous progress made in the recent decades, information has been relatively fragmented, providing only small snapshots of the Mediterranean deep-sea habitats, with most scientific studies having taken place after the development of deep-water fishery in the early decades of the 20th century [6]. Modern methods and technology, such as enhanced sledges and dredges, a range of specially constructed nets that are frequently employed in conjunction with many sensors, as well as video and camera systems, have made it possible to explore new areas, which has led to the discovery of new deep-sea communities [4,7–14].

Across all bathymetric zones, from the intertidal to the deep sea, on both hard and soft substrates, sponges (phylum Porifera) colonize a wide range of marine ecosystems [15]. Being structure-forming animals, sponges play a significant role in the functioning of marine benthic ecosystems [16,17]. Their erect growth form creates complex three-dimensional habitats, attracting numerous associated species of other invertebrates and fish [18–22]. Acting as ecosystem engineers, sponges promote local species diversity, which is very important in deeper ecosystems, where habitat heterogeneity decreases with increasing depth [23,24].

The Mediterranean basin is home to around 10% of the world's sponge species [25]. Sponges account for around 6% of the recorded invertebrate diversity in the Mediterranean [23] and 14.4% of the megabenthic invertebrate taxa reported as trawl bycatch from the Mediterranean soft-bottom grounds [26]. Even though in recent years the importance of sponges in deep-water Mediterranean ecosystems has been recognized, and sponge dominated deep-sea habitats are considered remarkable [1,27], the impacts of direct and indirect anthropogenic activities, such as bottom trawling and global climate change, on deep-sea sponge ecosystems have not yet been extensively studied [28,29]. Deep-sea sponge assemblages are considered "vulnerable marine ecosystems" (VME), a term coined by the United Nations to identify species, communities or habitats vulnerable to fishing activities [30]. Deep-sea sponge aggregations, developing on both hard and soft bottoms, have been listed as VME indicator taxa [31] due to their rarity, functional importance and sensitivity to both direct and indirect effects of human activities (such as bottom fishing). Recent research has shown that besides deep-sea sponge aggregations, the Mediterranean Sea is home to several distinctive VMEs, which show high vulnerability to disturbance and low recovery potential [32]. For the establishment of tools for environmental management of such areas, extensive knowledge of the biogeographic patterns of species and habitats is crucial [29].

Concerning sponges, their distribution in the Mediterranean is known to be quite uniform [33], but even though the Mediterranean sponge fauna is among the world's most studied [15], the knowledge is more or less limited to habitats shallower than 100 m, with the majority of the available information covering depths of 0–30 m, which can be easily reached with conventional diving techniques [34]. Over recent years, there has been a growing interest in the exploration of the mesophotic zone [10,14,21,30,35–40]. Yet available information about sponges in deeper habitats, even on basic community aspects, such as distribution, is quite limited [41] and mainly concerns the western Mediterranean [12,35,42–44]. In the Ionian ecoregion, research mostly relates to hard mesophotic substrates of the western part, such as deep-sea coral banks [45,46], marine canyons [41,47] and seamounts [44], while in the eastern Ionian Sea no such information exists. For the Aegean and the Levantine Seas, the scattered information on the mesophotic and deep-sea sponges was reviewed by Voultsiadou in 2005 [48], with the most recent data concerning sponges in mesophotic sites off the coast of Israel [10,49,50]. Despite the fact that several recent records of octocorals and sponges come from the deep eastern Mediterranean, there is scattered information on the existence of extensive assemblages of vulnerable deep-sea sessile invertebrates in the region, mostly collected decades ago, as pointed out by Salomidi et al. [32].

The aim of this work was to shed light on the diversity and distribution of sponge communities in mesophotic and deep-sea soft substrates of the eastern Mediterranean Sea, utilizing effectively, for the first time in the eastern Mediterranean, sampling material from fish stock monitoring programs. Specifically, we intend to provide information on the geographical, bathymetric and community composition patterns of sponges in the mesophotic and deep-sea soft bottoms of the eastern Mediterranean Sea, investigating areas which have remained largely understudied regarding their sponge fauna.

2. Materials and Methods

2.1. Study Area

Field surveys were carried out with experimental and commercial bottom trawls in the soft bottoms of the Aegean and the eastern part of the Ionian Sea ecoregion [51]. For the purposes of this study, the Aegean Sea was divided into five subareas (Figure 1) based on Voultsiadou [48]: the North Aegean (AgA), separated from the rest of the Aegean by the north Aegean trough; the Central-West Aegean (AgB), including the east coast of central Greece; the Central-East Aegean (AgC), including the Lemnos plateau and Chios basin; the South-West Aegean (AgD), including the Cyclades plateau and Saronikos Gulf; and the marine area around Kythira Island, being transitional between the Aegean and the Ionian Sea. The part of the Ionian Sea examined was divided into four subareas corresponding to its main geographical divisions (Figure 1): the North Ionian (IoN), spanning from Corfu Island to the Lefkas–Cephalonia islands strait; the Central Ionian (IoC), from the above mentioned strait to the Zakynthos–Kilini Strait, including the Patraikos Gulf; and the South Ionian (IoS), from the Zakynthos–Kilini Strait to the Messiniakos Gulf. The Korinthiakos Gulf, although usually referred to as part of the Ionian Sea, was examined separately from the rest of the Ionian Sea, as it is a small, deep and long semi-enclosed marine area connecting the Ionian with the Aegean Sea.

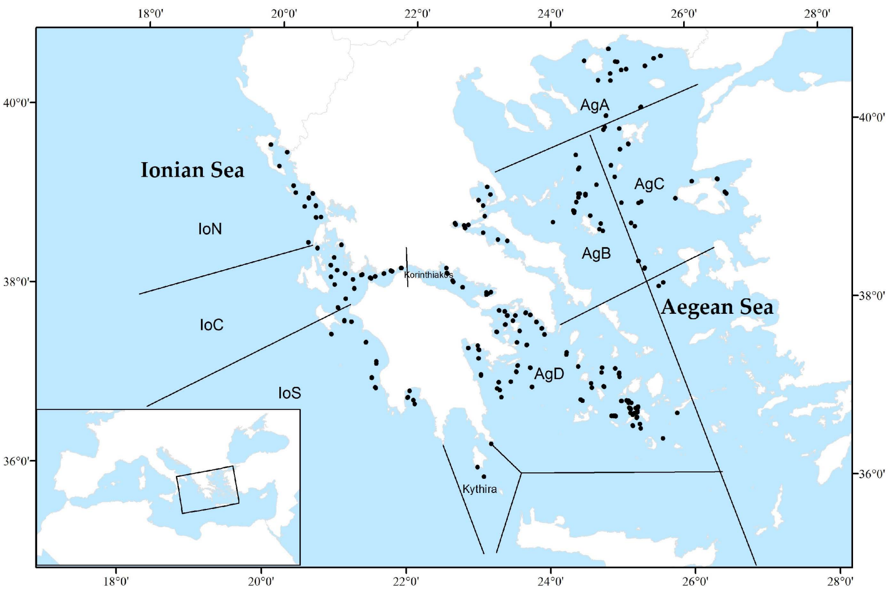

Figure 1. Map of the sampling stations in both studied ecoregions. Bottom left corner: the location of the study area (Aegean and Ionian Sea ecoregions) in the Mediterranean Sea. AgA—North Aegean; AgB—Central-West Aegean; AgC—Central-East Aegean; AgD—South-West Aegean; Kythira—the marine area around Kythira Isl.; IoN—North Ionian; IoC—Central Ionian; IoS—South Ionian; and Korinthiakos—the Korinthiakos Gulf.

2.2. Sampling

Sponge material was collected using bottom trawls. The bulk of the material was collected from experimental bottom-trawl fishing, as part of two fish-stock monitoring programs conducted from 2016 to 2018. Aiming at maximizing the spatial coverage of the study, sponge material collected with commercial bottom trawls during fish-stock monitoring programs was also examined. The programs from which the sponge material derived were the "Mediterranean Trawl Survey" (MEDITS) and the "Implementation of integrated marine water monitoring program" (IIMWM) in the case of the experimental fishing sampling, and the "Data Collection Framework" (DCF) in the case of the commercial bottom fishing sampling. A total of 282 stations were sampled with a bottom trawl in a random sampling scheme, on soft bottoms, covering a total area of 26.42 km^2 in the Aegean Sea and 5.93 km^2 in the Ionian Sea, and five depth strata from the lower sublittoral to the bathyal zone: 10–50 m, 50–100 m, 100–200 m, 200–500 m and 500–800 m. Sampling stations are depicted in Figure 1 and information about area, subarea, depth zone, year of sampling and survey for each station is provided in Table S1.

The MEDITS survey is carried out annually following a standardized protocol in various areas of the Mediterranean Sea, and its primary goal is to monitor changes in the abundance of demersal megafauna species. For the purpose of this study, material from the MEDITS survey conducted in the Aegean and the east Ionian Sea for the years 2016 and 2018 was examined. A total of 201 stations from the MEDITS survey were considered (110 in the Aegean Sea and 91 in the Ionian Sea). The duration of sampling at each station (haul) was 30 min on the continental shelf (10–200 m depth) and 60 min on the slope (201–800 m depth). The bottom trawl codend mesh size was 20 mm diamond and the standard fishing speed was 3 knots on the ground.

Material from 13 stations was also collected with an experimental bottom trawl (codend mesh size, 23 mm diamond) in four areas of the Central-West Aegean (AgB), namely the North Evoikos Gulf, Malliakos Gulf, Oreoi Strait and Pagasitikos Gulf, at depths between 23 and 160 m in the frame of the IIMWM program. Two of the former gulfs, Pagasitikos and Malliakos, are permanent Fisheries Restricted Areas (FRAs), while the North Evoikos Gulf is a seasonal FRA, in which fishing with towed gears, such as bottom trawls, has been prohibited since 1966 [52]. The duration of sampling at each station during the IIMWM program ranged from 45 min to a maximum of 90 min.

The additional sponge material was collected from 66 commercial bottom trawl hauls during sampling for the European Data Collection Framework (DCF) in the South-West Aegean (AgD) during October 2016 and October 2018. Two commercial bottom trawls (codend mesh size, 40 mm diamond) operated at depths of between 50 and 460 m. The duration of sampling at each station ranged from 1.5 h to a maximum of 6 h.

The difference between the sampling gears used in experimental and commercial sampling was deemed acceptable by the authors, given the large body size of the organisms under study and the fact that all official estimates of fish stock combine both experimental and commercial fishing methods [53].

At each station (haul) sponges were separated from the rest of the catch (Figure 2), counted, wet weighted (kg) and stored for further analysis. The collected sponge samples were preserved either in 4% formaldehyde solution or 90% ethanol solution, or they were stored in the freezer, depending on sampling conditions during the different sampling expeditions. The encrusting sponges found attached on rocks or on biogenic origin material were excluded from this analysis due to difficulties, mostly lack of time, in handling this kind of material onboard. Sponge abundance and biomass were expressed per square kilometer in order to safeguard a smooth comparison between the different swept areas of the partial sampling (derived from the different gear characteristics and duration).

Figure 2. Examples of typical sponge samples caught in trawl hauls after the onboard sorting procedures.

2.3. Sample Processing

Permanent microscope slides of histological sections and skeletal elements (spicules) were prepared using the protocol suggested by Hooper [54], while the classification followed was that proposed by Hooper and van Soest [55] in Systema Porifera and updated in the World Porifera Database [56]. Sample processing took place in the Research Laboratory of Marine Biology in the Department of Zoology at the Aristotle University of Thessaloniki. Sponge specimens were classified to the lowest possible taxonomic level. Sponge specimens and spicule preparations have been deposited in the Museum of the Department of Zoology, School of Biology, Aristotle University of Thessaloniki.

2.4. Data Analysis

The structure of sponge assemblages was analyzed by calculating several community metrics. For each station we estimated species richness, biomass/km^2, abundance/km^2, Shannon diversity index (H′), relative abundance, and biomass (the sponge abundance and biomass at each station to the total abundance and biomass collected).

The following metrics were estimated for each sponge taxon: presence (P)—the number of stations in which each species was found; frequency (F)—the percentage presence;

total biomass (B) expressed in kg/km^2; total abundance (A) expressed in specimens/km^2; mean dominance in terms of biomass (mDb)—the percentage of species biomass in relation to the total sponge biomass; mean dominance in terms of abundance (mDa)—the percentage of species abundance in relation to the total sponge abundance.

Multivariate analyses were used to compare similarity among sponge communities from different sampling areas and depth zones using log-transformed numerical data. Similarity matrices were constructed for both biomass and abundance data and nonmetric Multi-Dimensional Scaling (nMDS) based on Bray–Curtis similarity was applied to investigate resemblance patterns between sampling stations. Two-way similarity of percentage analysis (SIMPER) was used to identify the species responsible for the resemblance patterns observed. Multivariate analyses were performed with the PRIMER package [57].

Analysis of variance (GLM ANOVA) was used to examine differences in species richness, abundance and biomass among sampling stations and different depths using the Statgraphics package. Prior to the analyses, biomass and abundance data were transformed to $\chi' = \log(\chi + 1)$.

Species accumulative curves (SAC) were used for each depth zone and area, in order to test whether the research efforts could be a factor affecting the collected species richness.

3. Results

3.1. Sponge Diversity in the Two Ecoregions

Sponges were present in 156 out of the 280 sampling stations (55.7%). Specifically, in the Aegean Sea sponges were found in 102 of the 189 stations (53.9%), while in the Ionian Sea they were found in 54 of the 91 stations (59.4%).

A total of 1552 sponge specimens belonging to 87 taxa of 16 orders were examined (Table 1). All taxa identified were demosponges, except for one homoscleromorph (*Plakortis simplex*). The distribution of sponge abundance and biomass per sampling station (Table S1) is depicted in Figure 3. Photographs of the most common and some rare species are given in Appendix A.

Table 1. List of species found during the present study in the Aegean and Ionian Seas (organized alphabetically by class, order and species). F—frequency; mDb—mean dominance in terms of biomass; mDa—mean dominance in terms of abundance. Superscriptions: a—new records for the Aegean Sea; b—new records for the east Ionian Sea; c—endangered and threatened species (Annex II of the Bern and Barcelona conventions); d—species whose exploitation is regulated (Annex III of the Bern and Barcelona conventions).

CLASS/Orders/Species	Aegean Sea	Ionian Sea	Depth (m)	F	mDb	mDa
DEMOSPONGIAE						
Agelasida						
Agelas oroides (Schmidt, 1864)	x		37–250	4.49	0.93	0.66
Axinellida						
Axinella cannabina (Esper, 1794) [c]	x	x	34–119	9.62	0.37	1.63
Axinella damicornis (Esper, 1794)	x		37–74	1.92	0.04	0.18
Axinella polypoides Schmidt, 1862 [c]	x		38–86	3.21	0.18	0.44
Axinella sp.1	x		38–43	0.64	0.00	0.07
Axinella sp.2	x		65–118	1.28	0.01	0.15
Axinella verrucosa (Esper, 1794)	x	x	38–154	2.56	0.19	0.40
Raspailia (*Raspailia*) *viminalis* Schmidt, 1862	x	x	34.5–210	5.77	0.01	0.65
Raspailiidae sp.	x	x	24.7–53.7	3.21	0.10	0.27

Table 1. *Cont.*

CLASS/Orders/Species	Aegean Sea	Ionian Sea	Depth (m)	F	mDb	mDa
Bubarida						
Acanthella acuta Schmidt, 1862	x		26.3–101	5.77	6.36	18.01
Bubaris sp.	x		85–166	1.92	0.01	0.07
Dictyonella incisa (Schmidt, 1880)	x		45.4–84.2	1.28	0.12	0.32
Dictyonella obtusa (Schmidt, 1862)	x		90–91	0.64	0.03	0.07
Chondrillida						
Chondrilla nucula Schmidt, 1862	x		40–163.4	2.56	0.73	3.09
Chondrosiida						
Chondrosia reniformis Nardo, 1847	x	x	26.3–118	7.05	5.76	16.68
Clionaida						
Cliona celata Grant, 1826	x	x	35–68.4	4.49	0.36	0.89
Desmacellida						
Desmacella annexa Schmidt, 1870 [b]	x	x	78–154	1.92	0.02	0.19
Desmacella inornata (Bowerbank, 1866) [b]	x	x	37–774	1.92	0.00	0.17
Dictyoceratida						
Dysidea avara (Schmidt, 1862)	x	x	37–74	7.69	1.41	1.84
Dysidea fragilis (Montagu, 1814)	x	x	53–91	1.92	0.02	0.15
Fasciospongia cavernosa (Schmidt, 1862)	x		40–113.7	2.56	0.97	1.10
Hyrtios collectrix (Schulze, 1880)	x	x	45.4–96	3.21	0.15	0.36
Ircinia paucifilamentosa Vacelet, 1961	x		65–74	1.28	0.06	0.13
Ircinia sp.	x		92–98	0.64	0.13	0.07
Ircinia variabilis (Schmidt, 1862)	x	x	37–334	10.26	22.12	4.98
Pleraplysilla spinifera (Schulze, 1879)		x	60–63	0.64	0.01	0.03
Sarcotragus foetidus Schmidt, 1862 [c]	x	x	38–185.6	12.82	22.38	4.32
Scalarispongia scalaris (Schmidt, 1862)	x	x	43–102	3.85	1.89	0.66
Spongia (*Spongia*) *nitens* (Schmidt, 1862)	x		40–45	1.28	0.46	0.41
Spongia (*Spongia*) *officinalis* Linnaeus, 1759 [d]	x	x	32–109	8.33	1.77	0.96
Spongia (*Spongia*) *virgultosa* (Schmidt, 1868)	x		43–48	0.64	0.04	0.07
Haplosclerida						
Haliclona (*Gelius*) sp.	x	x	65–113.7	3.21	0.05	0.37
Haliclona (*Haliclona*) *simulans* (Johnston, 1842)	x		45.4–100.8	3.21	0.04	0.26
Haliclona (*Reniera*) cf. *fulva*	x		136.8–173	0.64	0.00	0.06
Haliclona (*Reniera*) sp.1	x		45.4–166	5.13	0.30	1.39
Haliclona (*Soestella*) *mucosa* (Griessinger, 1971)	x		136.8–173	0.64	0.01	0.06
Haliclona sp.		x	76.6–83.9	0.64	0.05	0.07
Petrosia (*Petrosia*) *ficiformis* (Poiret, 1789)	x		43–84	1.92	0.41	0.82
Siphonochalina coriacea Schmidt, 1868 [a]	x		91–100	1.92	0.01	0.06
Poecilosclerida						
Chondropsidae sp.	x		40–45.4	0.64	0.05	0.17
Echinoclathria sp.	x		45–47	0.64	0.01	0.06
Echinoclathria translata (Pulitzer-Finali, 1978) [b]		x	62.5–77.2	1.28	0.01	0.14
Microcionidae sp.	x		85–87	0.64	0.01	0.03
Mycale (*Aegogropila*) *contarenii* (Lieberkühn, 1859)	x		50–54	0.64	0.00	0.06
Mycale (*Aegogropila*) *retifera* Topsent, 1924		x	100–103	0.64	0.04	0.07
Mycale (*Aegogropila*) *syrinx* (Schmidt, 1862)	x	x	45.4–113.7	3.21	0.12	0.50
Mycale (*Aegogropila*) *tunicata* (Schmidt, 1862)	x	x	43–65	1.28	0.02	0.14
Mycale (*Mycale*) *lingua* (Bowerbank, 1866)	x	x	42–48	1.92	0.08	0.29
Mycale (*Mycale*) *massa* (Schmidt, 1862)	x	x	26.3–91	7.69	2.21	5.01
Mycale sp.	x		51.8–54.5	1.28	0.01	0.11
Myxilla (*Myxilla*) *rosacea* (Lieberkühn, 1859)	x		45–99	4.49	0.40	0.87
Phorbas fictitius (Bowerbank, 1866)	x		40–45	0.64	0.01	0.08

Table 1. *Cont.*

CLASS/Orders/Species	Aegean Sea	Ionian Sea	Depth (m)	F	mDb	mDa
Phorbas posidoni Voultsiadou-Koukoura & van Soest, 1991	x		40–97	2.56	0.03	0.21
Phorbas sp.	x	x	43–77	2.56	0.33	0.68
Ulosa digitata (Schmidt, 1866)	x	x	23.6–843	20.51	0.74	2.20
Polymastiida						
Polymastia mamillaris (Müller, 1806) [a]	x		50–54	0.64	0.01	0.06
Suberitida						
Aaptos sp.	x		40–45.4	0.64	0.03	0.08
Axinyssa aurantiaca (Schmidt, 1864) [b]		x	42.8–77.2	1.28	0.17	0.14
Axinyssa sp.	x		120–129	0.64	0.14	0.05
Halichondria sp.	x		65–250.7	1.28	0.03	0.09
Halichondriidae sp.1	x	x	40–334	3.21	0.47	0.29
Halichondriidae sp.2		x	37–45	0.64	0.01	0.14
Hymeniacidon perlevis (Montagu, 1814) [b]		x	78–81	0.64	0.01	0.07
Hymeniacidon sp.	x		23.3–53.7	4.49	0.53	1.23
Laminospongia subtilis Pulitzer-Finali, 1983	x		273–334	0.64	0.00	0.03
Rhizaxinella elongata (Ridley & Dendy, 1886)	x	x	40–113.7	1.28	0.02	0.20
Rhizaxinella pyrifera (Delle Chiaje, 1828)	x	x	40–754	4.49	0.02	1.12
Spongosorites sp.		x	39–95	3.21	0.33	0.51
Stylocordyla pellita (Topsent, 1904) [b]		x	533–606	0.64	0.00	0.03
Suberites domuncula (Olivi, 1792)	x	x	32–225	16.03	0.35	6.00
Suberites ficus (Johnston, 1842)	x	x	41–154	7.69	0.82	1.83
Topsentia sp.1	x		110–285	1.92	0.03	0.10
Topsentia sp.2	x		397–563	2.56	0.23	0.08
Tethyida						
Tethya aurantium (Pallas, 1766) [c]	x		34–154	3.21	0.09	0.76
Tethya citrina Sarà & Melone, 1965 [c]	x		43–48	1.28	0.28	2.49
Tetractinellida						
Astrophorina sp.	x		748–754	0.64	0.00	0.03
Discodermia cf. *polymorpha* Pisera & Vacelet, 2011	x		110–173	1.92	0.03	0.79
Erylus discophorus (Schmidt, 1862)	x		136.8–309	1.28	0.10	0.09
Geodia cydonium (Linnaeus, 1767) [c]	x		26.3–154	3.85	12.4	0.87
Pachastrella monilifera Schmidt, 1868	x	x	100–724	8.33	2.66	0.39
Penares euastrum (Schmidt, 1868)	x		146–148	0.64	0.04	0.34
Penares helleri (Schmidt, 1864)	x		78.6–369	3.21	0.52	1.79
Stelletta grubii Schmidt, 1862	x		23.6–41	0.64	0.20	0.05
Stryphnus mucronatus (Schmidt, 1868)	x		43–265	1.28	0.24	0.08
Thenea muricata (Bowerbank, 1858)	x	x	92–342	7.05	0.02	4.61
Verongiida						
Aplysina aerophoba (Nardo, 1833) [c]	x	x	34–311	16.03	8.60	2.91
HOMOSCLEROMORPHA						
Homosclerophorida						
Plakortis simplex Schulze, 1880	x		500–525	0.64	0.00	0.02

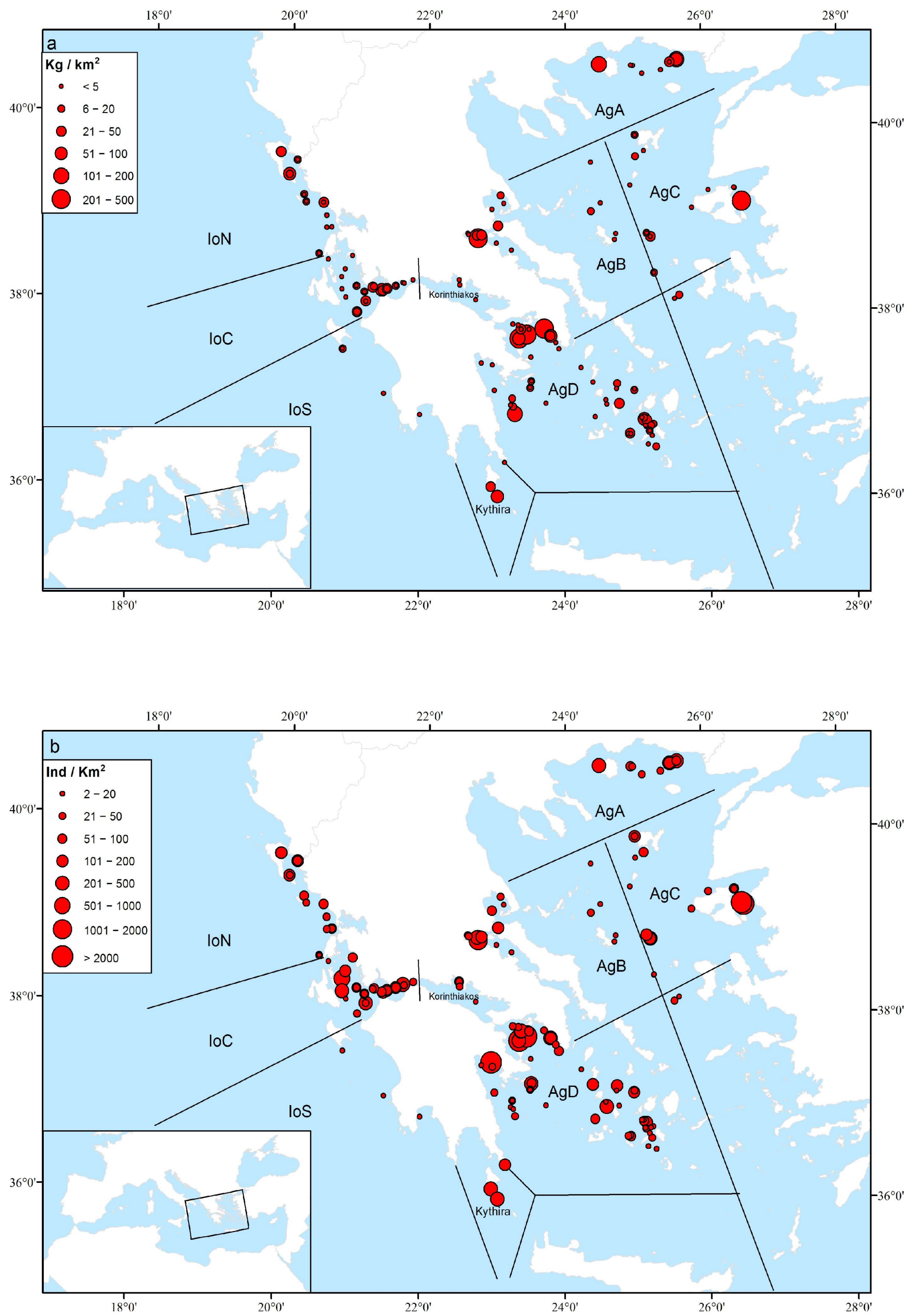

Figure 3. Sponge distribution in the sampling stations of both studied ecoregions in terms of (**a**) biomass (kg/km^2) and (**b**) abundance (specimens/km^2). Bottom left corner—the location of the study area (Aegean and Ionian Sea ecoregions) in the Mediterranean Sea. AgA—North Aegean; AgB—Central-West Aegean; AgC—Central-East Aegean; AgD—South-West Aegean; Kythira—the marine area around Kythira Isl.; IoN—North Ionian; IoC—Central Ionian; IoS—South Ionian; and Korinthiakos—the Korinthiakos Gulf.

Overall, 78 sponge species were found in 102 Aegean stations. Species richness per station varied from one to 29 species (Table S1). Over 35% of the sampling stations were inhabited by only one sponge species, 27.5% by two species, while in only 20% of the stations more than five species were found. In the Ionian Sea, a total of 39 demosponge species were collected in 54 stations. Over 40% of the stations examined had one species, around 30% two species, while in only 11% of the stations more than five sponge species were found (Table S1).

The most frequently found sponges over the entire study area were *Ulosa digitata* (20.5% of the sampling stations), *Aplysina aerophoba*, *Ircinia variabilis*, *Suberites domuncula* (16% frequency each) and *Sarcotragus foetidus* (12.8%) (Table 1). In the Aegean Sea the most common species were the keratose sponges *Ircinia variabilis* (21.57%), *Aplysina aerophoba* (19.61%) and *Sarcotragus foetidus* (18.63%) (Table S2), while in the Ionian Sea, *Ulosa digitata* and *Suberites domuncula* were the most frequently found species (frequency 37% and 20.37%, respectively) (Table S3).

3.2. Sponge Biomass and Abundance

Sponge biomass in the sampling stations ranged from 0.01 kg/km^2 to almost 1360 kg/km^2 (Figure 3a). In the Aegean Sea, subarea AgD showed the highest biomass (57.4% of the total Aegean Sea biomass), followed by subareas AgC (26.5%), AgB (8.6%), AgA (5.5%), while the lowest biomass was found in the Kythira subarea (2%). In the Ionian Sea, the highest biomass values were observed in subarea IoN (56.4% of the total Ionian sponge biomass), followed by IoC (35.2%) and IoS (7.6%), while the Korinthiakos Gulf subarea had the lowest biomass (0.9%). Most dominant in terms of biomass over the entire study area were the species *Sarcotragus foetidus*, *Ircinia variabilis* and *Geodia cydonium*, constituting 57% of the cumulative sponge biomass (Table S4). *Sarcotragus foetidus* (23.7%), *Ircinia variabilis* (22.9%) and *Geodia cydonium* (13.4%) accounted for 60% of the cumulative biomass in the Aegean Sea, while *Spongia officinalis*, *Aplysina aerophoba* and *Ircinia variabilis* accounted for almost half of the cumulative biomass in the Ionian Sea.

Abundance ranged between 2.6 and 5.4 specimens per km^2 (Figure 3b). In the Aegean Sea, the highest sponge abundance was found in AgD (62%), followed by AgC (23.6%), AgB (7.8%), AgA (3.7%) and Kythira (2.9%). In the Ionian Sea, the highest number of sponge specimens were collected in subarea IoC (63.5%), followed by IoN (30.7%), and the Korinthiakos Gulf (4.2%), while the lowest abundance value was found in subarea IoS (1.5%). The species *Acanthella acuta*, *Chondrosia reniformis*, *Suberites domuncula* and *Mycale massa* accounted for almost half of the cumulative abundance over the entire study area (Table S4). *Acanthella acuta*, *Chondrosia reniformis*, *Suberites domuncula* and *Ircinia variabilis* constituted almost half of the cumulative abundance in the Aegean Sea (Table S2), versus *Thenea muricata*, *Ulosa digitata*, *Suberites domuncula* and *Suberites ficus* in the Ionian Sea (Table S3).

3.3. Geographical and Bathymetric Patterns

Both sponge biomass and abundance varied significantly ($p < 0.05$) in the two different ecoregions and between depth zones (Tables S5 and S6), according to PERMANOVA results. The combination of area and depth zone also had a statistically significant effect on the above metrics. The Shannon diversity also varied significantly ($p < 0.05$) between depth zones and ecoregions (Table S7), with the values of the index decreasing with depth. The minimum value of the Shannon diversity index was found in depth zone 200–500 m and remained almost constant in the deeper zones (Figure 4a). Shannon diversity values were higher in the Aegean ecoregion (average of 0.49) than in the Ionian ecoregion (average of 0.34) (Figure 4b).

In the Aegean Sea, both subareas and depth factors showed statistically significant variability ($p < 0.05$) for all the community metrics examined, namely species richness (Table S8), biomass (Table S9), abundance (Table S10) and Shannon diversity (Table S11). A differentiation in terms of sponge species composition was also found, with different species dominating both in terms of biomass and abundance in each subarea (Table 2).

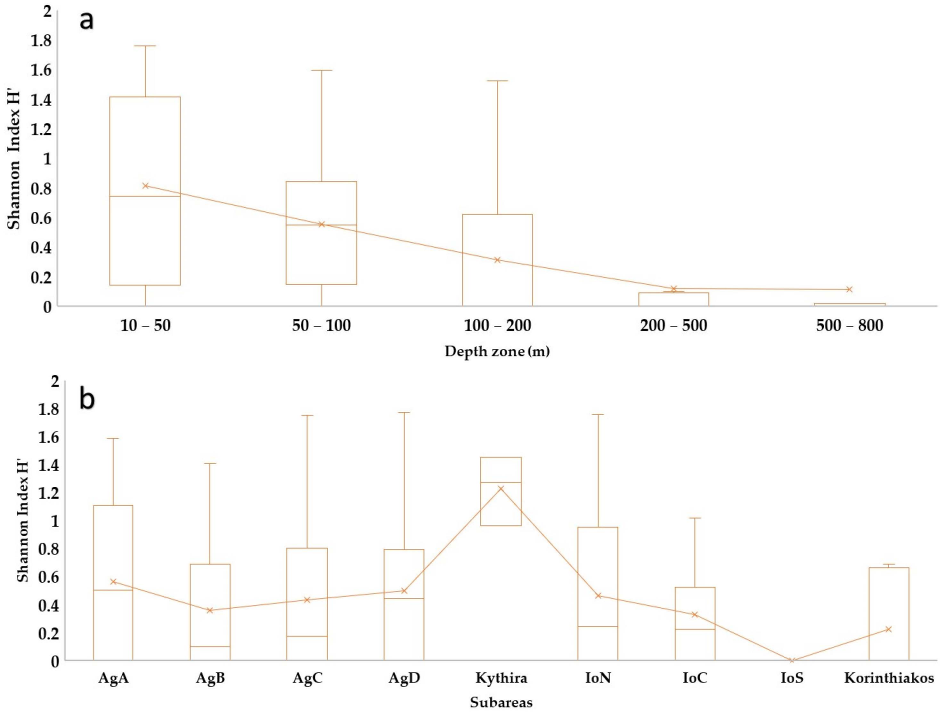

Figure 4. Box plots of Shannon diversity index by (**a**) depth zone and (**b**) subareas: AgA—North Aegean; AgB—Central-West Aegean; AgC—Central-East Aegean; AgD—South-West Aegean; Kythira—the marine area around Kythira Isl.; IoN—North Ionian; IoC—Central Ionian; IoS—South Ionian; and Korinthiakos—the Korinthiakos Gulf.

Table 2. Dominant sponge species in terms of biomass and abundance in the five Aegean subareas. Only species contributing 50% to cumulative dominance are presented: AgA—North Aegean; AgB—Central-West Aegean; AgC—Central-East Aegean; AgD—South-West Aegean; Kythira—the marine area around Kythira Isl.

		Biomass		
AgA	AgB	AgC	AgD	Kythira
Geodia cydonium (43.1%) *Ircinia variabilis* (28.8%)	*Geodia cydonium* (56.6%)	*Sarcotragus foetidus* (43.6%) *Geodia cydonium* (23.2%)	*Ircinia variabilis* (34.8%) *Sarcotragus foetidus* (19.9%)	*Ircinia variabilis* (34%) *Sarcotragus foetidus* (29.6%)
		Abundance		
AgA	AgB	AgC	AgD	Kythira
Cliona celata (13.9%) *Tethya aurantium* (10.8%) *Hymeniacidon* sp. (10.5%) *Ulosa digitata* (7.3%) *Geodia cydonium* (7.1%) *Ircinia variabilis* (5.5%)	*Mycale massa* (52.7%)	*Suberites domuncula* (17.8%) *Tethya citrina* (12.3%) *Penares helleri* (8.2%) *Sarcotragus foetidus* (8.1%) *Fasciospongia cavernosa* (5.1%)	*Acanthella acuta* (33.4%) *Chondrosia reniformis* (30%)	*Ircinia variabilis* (26.7%) *Sarcotragus foetidus* (19.5%) *Discodermia* cf. *polymorpha* (10.1%)

In the Ionian Sea, sponge species richness (Table S12), abundance (Table S13) and Shannon diversity (Table S14) differed significantly (95% confidence level) among the five depth zones examined, but not among subareas, according to GLM ANOVA analysis of variance. Sponge biomass differed significantly (95% confidence level) both among depth zones and subareas (Table S15). Although the four subareas of the Ionian Sea did not differ significantly with regards to sponge abundance and species richness, sponge biomass differed (more than 90% in all cases) in terms of species composition (Table 3).

Table 3. Dominant sponge species in terms of biomass and abundance in the four Ionian subareas. Only species contributing 50% to cumulative dominance are presented: IoN—North Ionian; IoC—Central Ionian; IoS—South Ionian.

Biomass			
IoN	IoC	IoS	Korinthiakos Gulf
Aplysina aerophoba (41.7%) *Spongia officinalis* (18.3%)	*Ircinia variabilis* (23.9%) *Spongia officinalis* (21.1%) *Suberites ficus* (14.2%)	*Pachastrella monilifera* (98.5%)	*Axinella verrucosa* (69.5%)
Abundance			
IoN	IoC	IoS	Korinthiakos Gulf
Suberites domuncula (3%) *Ulosa digitata* (12.3%) *Raspailia viminalis* (11.2%) *Aplysina aerophoba* (10.1%) *Spongosorites* sp. (9.9%)	*Thenea muricata* (44.9%) *Ulosa digitata* (9.8%)	*Pachastrella monilifera* (42.6%) *Suberites domuncula* (28.7%)	*Axinella verrucosa* (24.8%) *Ircinia variabilis* (24.5%)

In both ecoregions, the depth zone at 50–100 m was the richest in total species number (49 in the Aegean and 27 in the Ionian Sea), followed by the zone at 10–50 m (46 in the Aegean and 19 in the Ionian Sea). Species richness decreased with depth in both ecoregions (Figure 5). The lowest species number was recorded at 500–800 m in the Aegean Sea (five species) and at 200–500 m in the Ionian (only *Thenea muricata* was found). The most common species in the various depth zones varied by region (Tables 4 and 5).

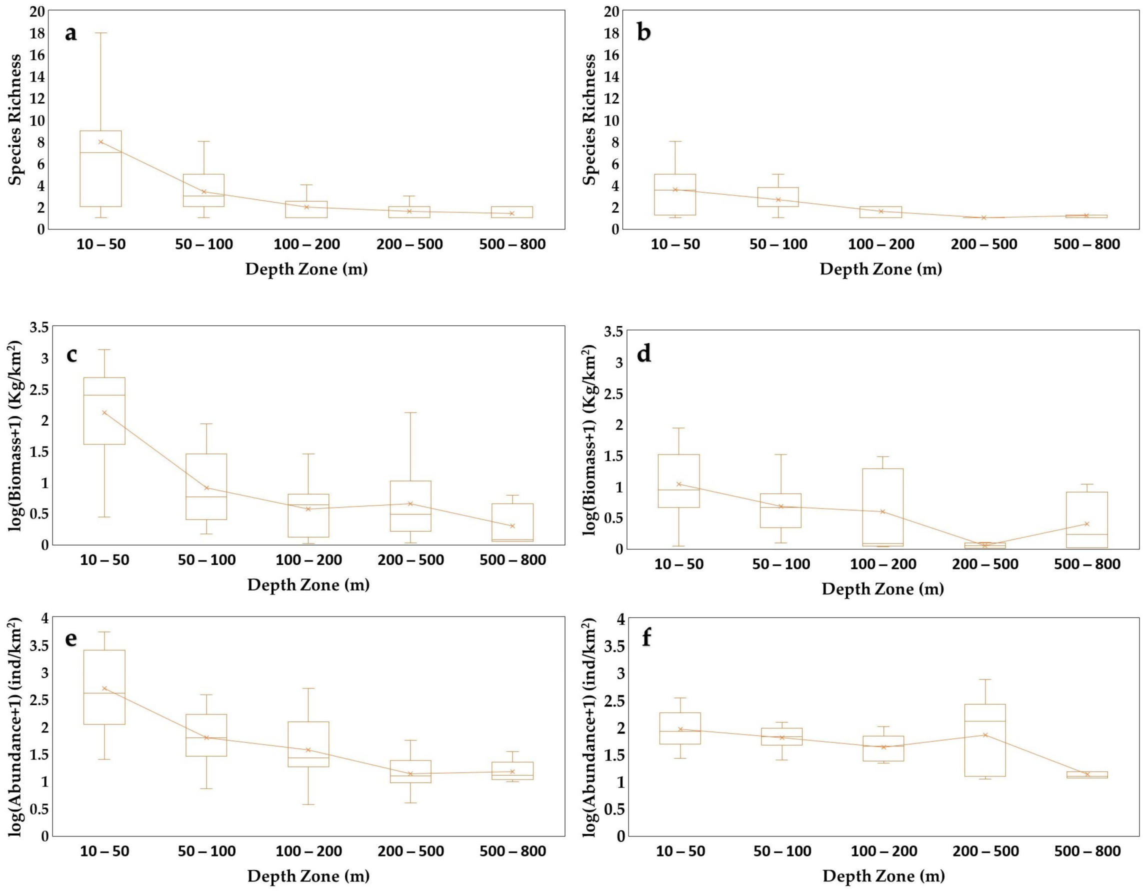

Figure 5. Box plots by depth zone for: (**a**) Aegean sponge species richness, (**b**) Ionian sponge species richness, (**c**) Aegean sponge biomass, (**d**) Ionian sponge biomass, (**e**) Aegean sponge abundance, and (**f**) Ionian sponge abundance.

Table 4. Dominant sponge species in terms of biomass and abundance in the five depth zones of the Aegean Sea. Only species contributing at least 50% to cumulative dominance are presented.

		Biomass		
10–50 m	50–100 m	100–200 m	200–500 m	500–800 m
Ircinia variabiliss (24%) *Sarcotragus foetidus* (23.8%) *Geodia cydonium* (14.8%)	*Sarcotragus foetidus* (29.8%) *Ircinia variabilis* (17.3%) *Geodia cydonium* (10.1%)	*Ircinia variabilis* (33%) *Sarcotragus foetidus* (32%)	*Pachastrella monilifera* (71.3%)	*Topsentia* sp.2 (95.1%)
		Abundance		
10–50 m	50–100 m	100–200 m	200–500 m	500–800 m
Acanthella acuta (26.6%) *Chondrosia reniformis* (24.5%)	*Haliclona* (*Reniera*) sp. (8.7%) *Suberites ficus* (7.8%) *Suberites domuncula* (7.7%) *Myxilla rosacea* (7.5%) *Sarcotragus foetidus* (6.8%) *Aplysina aerophoba* (6%) *Rhizaxinella pyrifera* (3.5%) *Agelas oroides* (3.4%)	*Penares helleri* (23.1%) *Ircinia variabilis* (12.8%) *Discodermia* cf. *polymorpha* (11%) *Thenea muricata* (5.1%)	*Pachastrella monilifera* (20.8%) *Thenea muricata* (12.1%) *Aplysina aerophoba* (10.4%) *Agelas oroides* (7.4%)	*Rhizaxinella pyrifera* (29.1%) *Topsentia* sp.2 (24.5%)
		Presence		
10–50 m	50–100 m	100–200 m	200–500 m	500–800 m
Aplysina aerophoba (P = 8) *Dysidea avara* (P = 7)	*Sarcotragus foetidus* (P = 9) *Aplysina aerophoba* (P = 6) *Myxilla rosacea* (P = 6)	*Haliclona* sp.1 (P = 4) *Ircinia variabilis* (P = 4) *Sarcotragus foetidus* (P = 4) *Suberites domuncula* (P = 4)	*Pachastrella monilifera* (P = 7)	*Pachastrella monilifera* (P = 2) *Topsentia* sp.2 (P = 2)

Table 5. Dominant sponge species in terms of biomass and abundance in the five depth zones of the Ionian Sea. Only species contributing at least 50% to cumulative dominance are presented.

		Biomass		
10–50 m	50–100 m	100–200 m	200–500 m	500–800 m
Aplysina aerophoba (39.9%) *Spongia officinalis* (30.4%)	*Ircinia variabilis* (35.8%) *Sarcotragus foetidus* (16.5%)	*Suberites ficus* (47.7%) *Spongia officinalis* (27.1%)	*Thenea muricata* (100%)	*Pachastrella monilifera* (99%)
		Abundance		
10–50 m	50–100 m	100–200 m	200–500 m	500–800 m
Ulosa digitata (17.6%) *Rhizaxinella pyrifera* (12.9%) *Spongia officinalis* (9.6%) *Aplysina aerophoba* (8.8%) *Spongosorites* sp. (7%)	*Suberites domuncula* (16.1%) *Ulosa digitata* (14.7%) *Mycale massa* (10.3%) *Ircinia variabilis* (8.9%)	*Suberites ficus* (34.6%) *Raspailia vimilaris* (20.9%)	*Thenea muricata* (100%)	*Pachastrella monilifera* (41.6%) *Ulosa digitata* (29.4%)
		Presence		
10–50 m	50–100 m	100–200 m	200–500 m	500–800 m
Ulosa digitata (P = 8) *Spongia officinalis* (P = 5) *Raspailia vimilaris* (P = 4)	*Ulosa digitata* (P = 9) *Suberites domuncula* (P = 6) *Mycale massa* (P = 4)	*Raspailia vimilaris* (P = 3) *Suberites domuncula* (P = 3)	*Thenea muricata* (only representative)	*Pachastrella monilifera* (P = 3) *Ulosa digitata* (P = 2)

Sponge biomass decreased with increasing depth in both ecoregions (Figure 5). The highest biomass values were found in the shallowest depth zone (10–50 m), while the lowest values were recorded at 500–800 m in the Aegean and at 200–500 m in the Ionian Sea. Dominant species in terms of biomass differed between the various depth zones (Tables 4 and 5). Sponge abundance also decreased with increasing depth in both ecoregions (Figure 5), with the lowest value recorded at 500–800 m depth. Different species dominated in terms of abundance among depth zones and between the two ecoregions (Tables 4 and 5).

3.4. Sponge Resemblance Patterns

No clear patterns of similarity between the two ecoregions or the different depth zones were found, according to MDS analysis based on the biomass and abundance data (Figure 6).

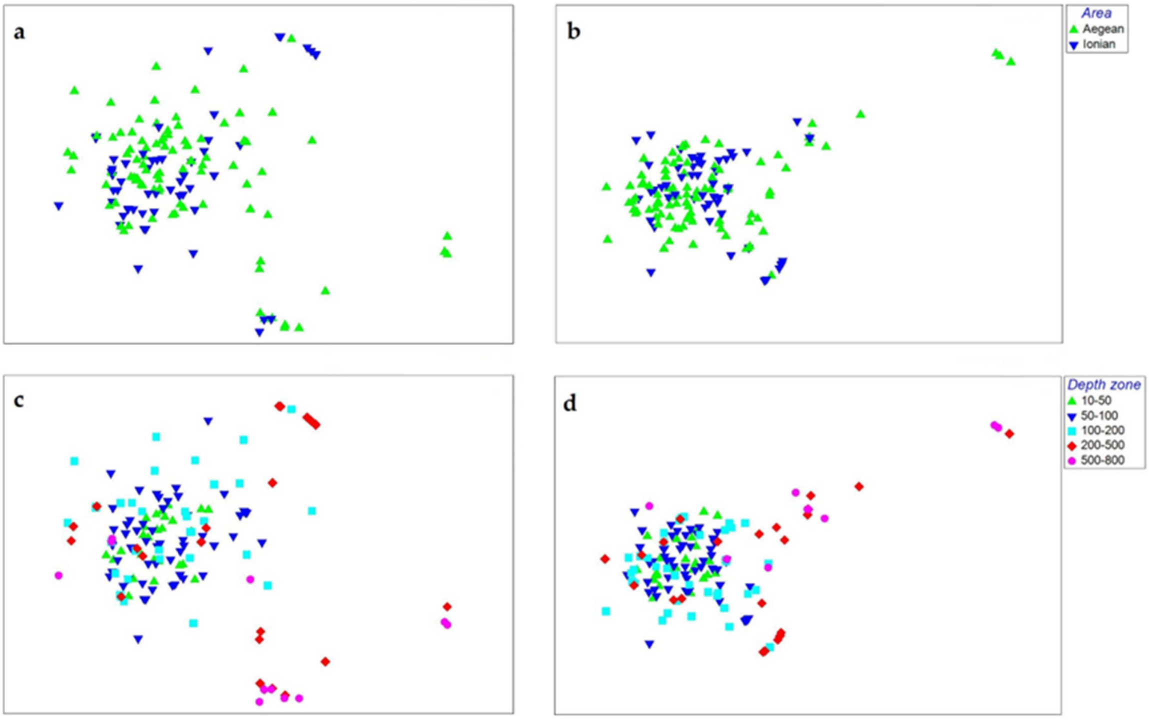

Figure 6. MDS showing two-dimensional resemblance of sponge community structures between the Aegean and Ionian Sea stations, based on: (**a**) biomass and (**b**) abundance; and between the different depth zones, based on: (**c**) biomass and (**d**) abundance.

SIMPER analysis revealed that the average percentage dissimilarity between the Aegean and Ionian stations was 95.54% based on biomass and 95.45% based on abundance. The Aegean Sea stations had an average similarity of 5% based on biomass and 4.6% based on abundance, while the Ionian Sea stations had a similarity of 8.9% and 9.6% for biomass and abundance, respectively. Four sponge species, *Ircinia variabilis*, *Sarcotragus foetidus*, *Aplysina aerophoba* and *Pachastrella monilifera*, contributed 54% of the similarity between stations of the Aegean Sea in terms of biomass, while in terms of abundance, five species, *Ircinia variabilis*, *Suberites domuncula*, *Sarcotragus foetidus*, *Aplysina aerophoba* and *Pachastrella monilifera* contributed 58.8%. In the Ionian Sea, two sponge species, *Ulosa digitata* and *Suberites domuncula*, contributed to the similarity among stations almost 56.5% and 59.6% based on biomass and abundance, respectively.

3.5. Sponge Diversity and Research Effort

Species accumulation curves (Figure 7) were constructed in order to check whether the sampling efforts affected the species numbers and whether the results of the study were representative of the existing sponge communities. The above mentioned curves gave the following results: (i) the number of species collected at depths shallower than 500 m in the Aegean Sea seems to be representative of the total sponge fauna, since the curves tend to become asymptotic; (ii) the curves for the two shallowest depth zones (10–50 and 50–100 m) of the Aegean show an initial abrupt increase, while all the other curves in both areas are smoothly increasing; (iii) in the Ionian Sea, only the curve for the depth zone at 50–100 m tends to become asymptotic, showing adequate species collection; iv) in the deepest zones (500–800 m) of both areas, very small numbers of species were found, so that a cumulative pattern is difficult to detect.

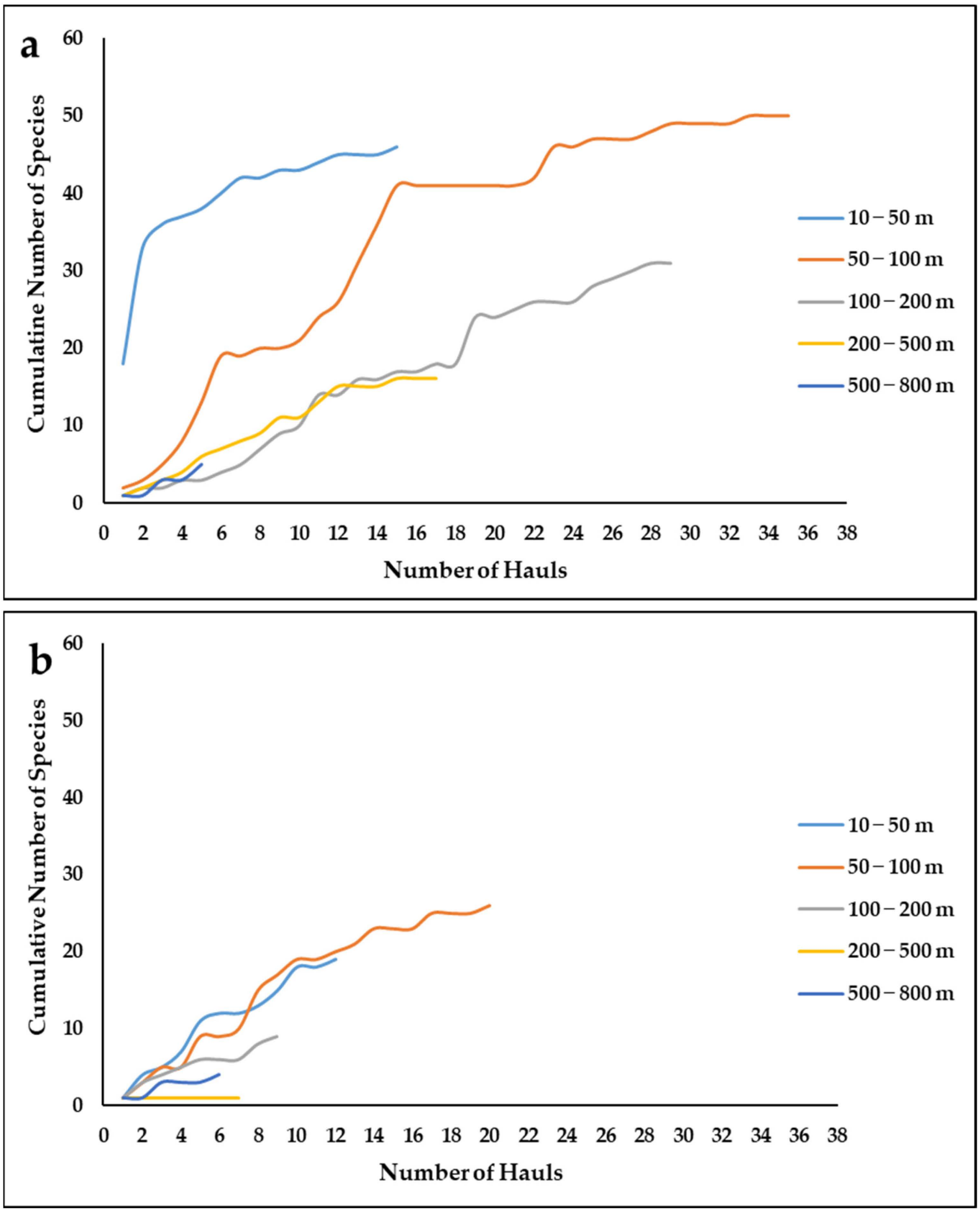

Figure 7. Species cumulative curves per depth zone for (**a**) Aegean Sea and (**b**) Ionian Sea.

4. Discussion

The Mediterranean basin is considered a hotspot of sponge diversity [15,29]. Nevertheless, little is known about sponge community structure in the soft, mesophotic and deep-sea bottoms of the Aegean and Ionian Seas. In this study, material collected in the framework of three programs, including MEDITS, offered a great opportunity to gain knowledge of these unexplored environments. Diversity, biomass and abundance data were collected and used for a first description of these sponge communities.

4.1. Sponge Diversity in the Two Ecoregions

The poriferan orders Suberitida, Poecilosclerida, Dictyoceratida, Tetractinellida, Axinellida and Haplosclerida presented the highest number of species, contributing 83% of the species in the studied ecoregions, in agreement with the latest (2016) updated checklist of the Porifera of Greece by Voultsiadou et al. [58], where the same orders (with the exception of Axinellida) dominated in terms of species number, constituting 62% of the sponge species richness.

The order Tetractinellida seemed to be more diverse in depths greater than 100 m, while in shallower soft bottoms (<200 m) Poecilosclerida and Dictyoceratida were the dominant orders in both ecoregions. The order Suberitida was more diverse between 50 and 500 m in the Aegean Sea, while in the Ionian Sea the same order had more representatives in shallower depths (10–100 m). Six orders (Agelasida, Bubarida, Chondrillida, Homosclerophorida, Polymastiida and Tethyida) were not represented at all in the material from the Ionian Sea.

The vast majority of sponge species identified in this study were already known as elements of the Aegean poriferan fauna [48,58], while two species (*Polymastia mamilaris* and *Siphonochalina coriacea*) are newly recorded for the Aegean Sea and six species (*Axinyssa aurantiaca*, *Desmacella annexa*, *D. inornata*, *Echinoclathria translata*, *Hymeniacidon perlevis* and *Stylocordila pellita*) are first recorded from the east Ionian Sea (Table 1).

The sporadic records of several species in the eastern Mediterranean up to date could be associated with the limited research in certain marine areas or types of habitats. Thus, increasing research efforts could enhance our knowledge of their populations and consequently modify the conservation status of some species by expanding not only their bathymetric but also their geographic distribution [34]. In the present study, nine individuals of the Aegean endemic species *Phorbas posidoni* were found in Cyclades plateau and Saronikos Gulf down to 97 m depth. This finding significantly expands the known distribution of the species since it was described with only one specimen by Voultsiadou-Koukoura and Van Soest [59] in the Kavala Gulf, north Aegean Sea, at a depth of 30 m. Furthermore, *Ircinia paucifilamentosa*, an Aegean Sea endemic species known from eight localities down to 40 m depth in marine caves and coralligenous habitats [34,60], was here found on soft bottoms of the Saronikos Gulf (AgD) between 60 and 74 m depth. Moreover, the Mediterranean endemic *Echinoclathria translata* is herein reported for the first time in the Ionian Sea and for the second time in the Aegean Sea and eastern Mediterranean [61]. The present study also extends the known bathymetric limit of the latter species from 40–50 m to 77 m depth. Similarly, *Stylocordila pellita* and *Axinyssa aurantiaca* are reported here for the first time in the east Ionian Sea and for the second time in the Aegean Sea [48,62]. Another rare species, *Laminospongia subtilis*, is reported here for the second time in the Aegean Sea, expanding its known bathymetric range down to 334 m in depth (the previous reported depth by Kefalas et al. [63] was 70 m). Such findings are critical for the conservation status of sponges like *P. posidoni* and *I. paucifilamentosa*, which have been characterized as data deficient in the Aegean ecoregion due to the limited available information [34]. In addition, *Spongia officinalis* was found to be the dominant species in terms of biomass in the Ionian ecoregion, even though, to date, quantitative information about this species in Greek seas derives mainly from the Aegean ecoregion [64,65].

Several species in the collected material have not yet been identified to species level (seventeen were identified to the genus level, five to the family level and one to the suborder level (Table 1)), possibly indicating the existence of rare or even new species. In addition, the future examination of small-sized encrusting sponges found on trawled pieces of hard sediments (e.g., rocks, litter or hard substrata of biogenic origin), which were excluded from this study, would probably reveal additional inconspicuous diversity which is also affected by trawling activity.

4.2. Sponge Geographical and Bathymetric Patterns

Sponge fauna in the Mediterranean basin has been shown to vary regionally, following an NNW-SSE impoverishment gradient in terms of species richness, due to (a) the different oceanographic features within this semi-enclosed sea [66–68] and (b) the generally low dispersal capacity of sponge larvae [69–72]. In this study, sponge community structure and diversity differed between the two ecoregions under investigation. As it has been proposed in previous studies [33,67], sponge distribution patterns may be affected by the different oceanographic features of the two ecoregions, although they extend over a similar range of latitude.

A higher number of species was found in the Aegean compared with the east Ionian Sea (78 versus 39 species). Even though greater research efforts (in terms of station numbers and covered area) took place in the Aegean Sea, the species accumulative curves showed that the higher number of species found in this area, in comparison with the Ionian, was not only a consequence of the greater number of hauls. The smoother curve growth in the latter, in comparison with the former, indicated poorer sponge diversity. Specifically in the depth zone 50–100 m, in which almost equal numbers of hauls were taken in both areas, one can see that in the Aegean a considerable number of species was obtained very early, in contrast with the Ionian where a smooth growth was observed. The predominance of the Aegean Sea in terms of sponge diversity, at least in the shallower depth zones, could be attributed to a certain degree to its unique geomorphological features. The Aegean Sea is characterized by an extensive coastal relief and continental shelf, a wide number of islands and insular clusters [73], as well as numerous smaller or larger flat-bottomed basins [74], providing sufficient vital space for the development of rich benthic communities. On the other hand, the Ionian Sea has a narrower continental shelf [74] and is characterized by a sharp increase in depth and an extended abyssal plain, which greatly restricts the hard substrate habitat favorable for sponges. This view is further strengthened by the fact that in the deep depth zones the cumulative sponge diversity was equally poor in both areas. Moreover, some subareas showed notably high diversity values despite limited research efforts. For example, although Kythira subarea had the fewest sampling stations (only three), it presented the highest estimated diversity values (Figure 4b). This could be attributed to its unique oceanographic (rich funneled waters through the straits connecting Kythira with the Aegean Sea) and geomorphological (high variety of seabed types) characteristics, which make it an area of high biological interest, as reported by Smith et al. [75]. These authors reported notable sponge and anthozoan populations in this subarea using ROV. The higher megabenthic diversity (including sponges) of the Aegean over the Ionian Sea was recently highlighted in a review about megabenthic invertebrates from trawlable soft bottoms [26].

Species richness did not differ statistically significantly between the subareas, but GLM ANOVA showed a clear distinction between the five depth zones for both ecoregions, with the number of species decreasing with depth. This is in agreement with previous studies, both those concerning sponges [76] and those regarding generally megabenthic invertebrates [26]. As expected, species with large body size and massive growth forms dominated in most depth zones. In both ecoregions, the depth zone of 50–100 m was the richest in terms of total species richness, followed by the shallowest depth zone at 10–50 m. These results highlight that the mesophotic zone in the eastern Mediterranean Sea is of high importance in terms of sponge diversity. This is probably related to the fact that the environmental conditions of the mesophotic zone are quite stable as it lies beneath the seasonal thermocline [77]. Along with the low lighting that prevents algal development, this makes the mesophotic zone an oasis for sponge communities [10].

4.3. Sponge Community Resemblance Patterns

The absence of clear resemblance patterns in sponge community structure in the Aegean Sea observed in the recent study was also reported by Kefalas et al. [63], who worked on trawled material from the lower sublittoral zone (30–130 m). However, Voultsiadou [48] found that the north Aegean subareas (AgA, AgB and AgC) were separated from the south Aegean subareas (AgD in our case), forming a distinct group with 59% similarity among them. This differentiation could be explained as follows: (a) Different data sets were processed, since Voultsiadou [48] used semiquantitative values of abundance based on data derived from the literature. (b) The data used by Voultsiadou [48] came from different substrates, some of which were in the shallow, rocky sublittoral zone (0–30 m) and not deeper than 350 m, while in the present study specimens were derived exclusively from soft bottoms down to 800 m, hence including deep-water habitats. As a consequence, it is possible that the complexity of shallow-water ecosystems drives the differentiation between the north and the south Aegean, while sponge communities in the deeper waters are more uniform. This is corroborated by the fact that in Voultsiadou [48] 19 species contributed to 50% of the ingroup similarity, while in the present study only five species (including the deep-sea sponge *Pachastrella monilifera*) contributed to 50% of the ingroup similarity among Aegean stations. In our study, Suberitida was the most diverse order in the Aegean (between 50 and 500 m) and the Ionian (between 10 and 100 m), while it is the fifth most speciose order of the phylum Porifera generally in the Greek Seas [58]. This can be explained by the fact that it includes various typical soft bottom species, which was the prevailing type of substrate in our case.

In the depth zone at 200–500 m, *Thenea muricata* was the only species found in the Ionian Sea. Monospecific assemblages of *T. muricata* have also been reported from the western Mediterranean sandy bottoms of the shelf break [35]. There are only a few Mediterranean sponge species which are specific to soft substrates (e.g., *Rhizaxinella* spp. and *Thenea muricata*) [78,79] but Kefalas et al. [63] listed a small group of species showing a certain preference for growing on soft substrates (i.e., *Tedania anhelans*, *Mycale syrinx*, *M. rotalis* and *M. massa*). In our study, two of these species, *M. syrinx* and *M. massa* were reported in 19 stations (six in the Ionian and 13 in the Aegean Sea). Three more species, namely *Ulosa digitata*, *Suberites domuncula* and *Raspailia vimilaris*, were found during our research to be quite common on soft bottoms of the Ionian and Aegean Seas.

Despite the absence of any clear resemblance patterns based on sponge biomass or abundance, the Ionian stations were positioned closer (revealing higher similarity), when compared to those of the Aegean ecoregion (Figure 6).

4.4. Vulnerable and Endangered Sponge Species

Considering the engineering activity of sponges and the microhabitats they offer to associated organisms, the investigation of sponge-rich sites and sponge grounds in the eastern Mediterranean mesophotic zone is crucial for conservation planning. In this sense it is interesting that eight of the species collected (Table 1) have been included in the lists of endangered and threatened species (Annex II) of the Bern Convention on the Conservation of European Wildlife and Natural Habitats, and the Barcelona Convention Protocol Concerning Specially Protected Areas and Biological Diversity in the Mediterranean [34].

Based on recent studies [43,80], sponge grounds are defined as aggregations where sponge density is equal or higher than 0.5 specimens/m^2. Although our values are much lower than this threshold, it is possible that sponge abundance in specific parts of the trawled bottom surface was underestimated because of our sampling method, since sessile invertebrates, such as sponges and anthozoans, have patchy distribution in deep waters [14,32,81]. Thus, the use of data from bottom trawls and the extrapolation per square kilometer could cause underestimation of sponge abundance, especially in localized "sponge gardens". The high sponge biomass values (>400 kg/km^2) found in several Aegean Sea sampling stations (Table S1), indicate the possible existence of such areas in three Aegean subareas (AgA, AgC and AgD). Considering that trawling is one of the main threats affecting sponge communities in the Aegean Sea [34], it is crucial to define regional thresholds for sponge dominated VMEs.

5. Conclusions

Typically, the aim of scientific bottom trawl surveys is to gather information on the distribution of a variety of fish species, as well as to estimate their relative abundance and other biological characteristics. However, for several species (mainly noncommercial invertebrates or bycatch species) for which information is scarce, trawl surveys (such as the MEDITS trawl survey) can be used as a primary tool for providing useful information on structural and biological parameters [82]. The present study is an example of the comprehensive use of such research resources and effort. Herein, we managed to make the most out of research cruises that were intended to study mainly fish stocks and we gained information about a poorly known part of the eastern Mediterranean marine ecosystem.

Overall, this study sheds light on the seldom investigated sponge communities in the mesophotic and deep-sea grounds of the eastern Mediterranean Sea, indicating the potential for new discoveries in the area.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/jmse11112204/s1, Table S1. Quantitative distribution of sponge species per sampling station; Table S2. Community parameters for the sponge communities of the Aegean Sea; Table S3. Community parameters for the sponge communities of the Ionian Sea; Table S4. Total community parameters of sponges in the Aegean and Ionian Seas; Table S5. PERMANOVA test results for sponge biomass between Aegean and Ionian Sea (Area) and depth zone. * indicates significant differences at $p < 0.05$; Table S6. PERMANOVA test results for sponge abundance between Aegean and Ionian Sea (Area) and depth zone. * indicates significant differences at $p < 0.05$; Table S7. General Linear Models Table of results for sponge diversity index H'. * indicates significant differences at $p < 0.05$; Table S8. General Linear Models Table of results for sponge species richness in the Aegean Sea. * indicates significant differences at $p < 0.05$; Table S9. General Linear Models Table of results for sponge species biomass in the Aegean Sea; Table S10. General Linear Models Table of results for sponge species abundance in the Aegean Sea. * indicates significant differences at $p < 0.05$; Table S11. General Linear Models Table of results for sponge diversity index H' in the Aegean Sea *indicates significant differences at $p < 0.05$; Table S12. General Linear Models Table of results for species richness in the Ionian Sea. * indicates significant differences at $p < 0.05$; Table S13. General Linear Models Table of results for sponge abundance in the Ionian Sea. * indicates significant differences at $p < 0.05$; Table S14. General Linear Models Table of results for sponge biomass in the Ionian Sea. * indicates significant differences at $p < 0.05$; Table S15. General Linear Models Table of results for sponge diversity index H' in the Ionian Sea. * indicates significant differences at $p < 0.05$.

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Appendix A

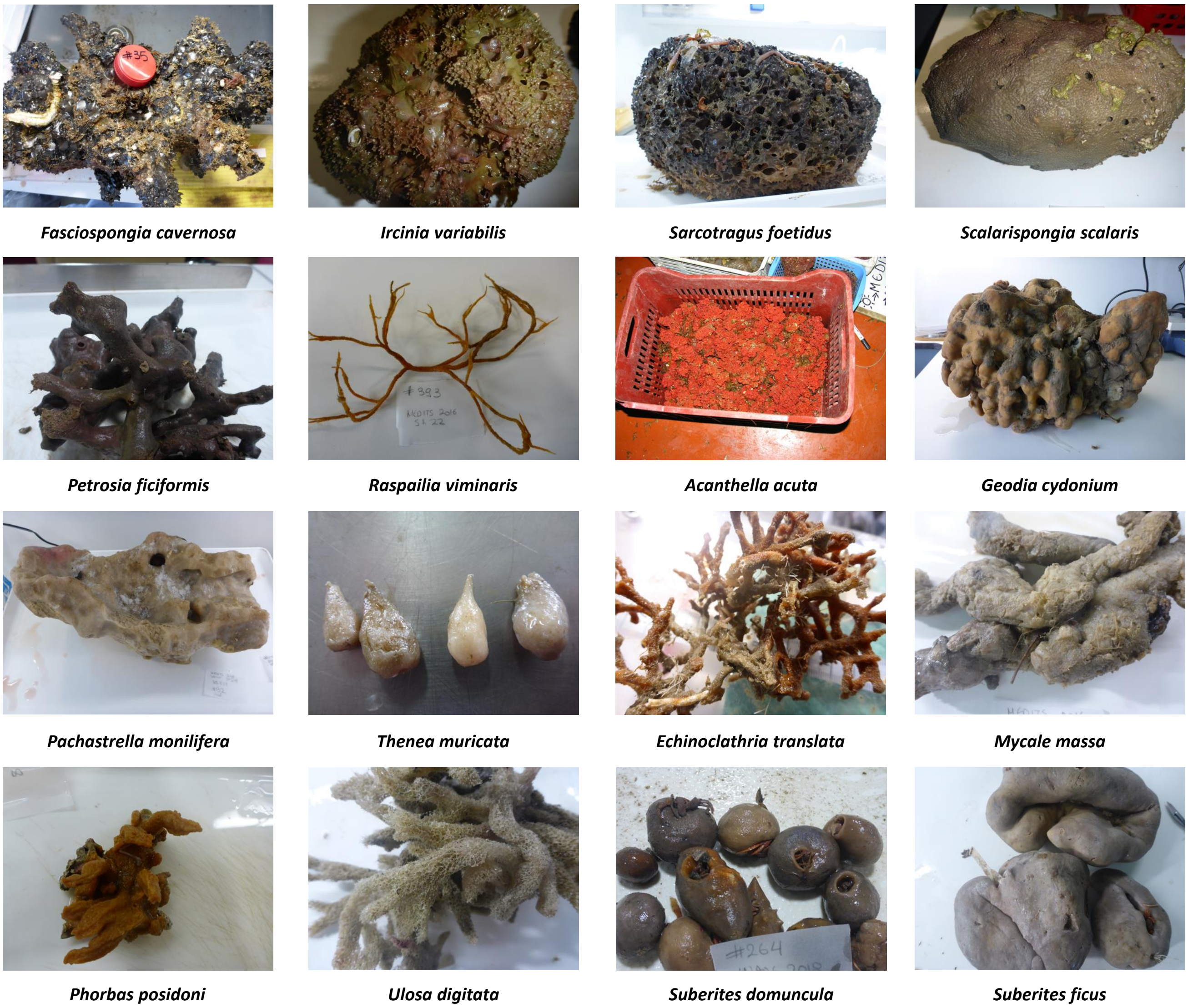

Figure A1. Photographs of the most common and some rare species found on the mesophotic and deep-sea soft bottoms of the Aegean and east Ionian Sea.

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