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Census of biodiversity in marine caves of the eastern Mediterranean Sea

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Abstract

Scientific information on the biodiversity of marine caves in the eastern Mediterranean is limited, especially when considering the extensively studied caves of the north-western and central Mediterranean. Aiming to enhance current knowledge regarding cave communities, this study represents a first assessment of the marine cave biota of the eastern Mediterranean, as defined by the European Union's Marine Strategy Framework Directive (MSFD). Information retrieved from an extensive overview of relevant scientific documents was combined with original data recorded from 23 marine caves in the north-eastern Mediterranean. Our results report a total of 520 taxa recorded in eastern Mediterranean marine caves to date, the majority of which are sponges, polychaetes, rhodophytes, bivalves, fishes, and gastropods. These include several protected, endemic and alien species. However, not all taxonomic groups from different areas have been equally investigated and future studies are expected to increase the number of endemic and alien species. The observed general trend is that the reported species number is generally related to sampling effort and scientific expertise. The most well-studied marine cave communities in the eastern Mediterranean are those of the Aegean Sea (especially its northern sector), which presented the highest number of species, followed by those of the Levantine. Furthermore, our research in Aegean caves revealed numerous new records for the marine cave fauna of the eastern basin, while several species are reported for the first time in a marine cave habitat. The critical need for further scientific research, monitoring, and conservation of this unique ecosystem was highlighted by (i) the presence of certain species endemic to the eastern Mediterranean coupled with a high proportion of alien species, especially in the Levantine Basin, and (ii) marine cave habitat availability in isolated insular areas of the eastern Mediterranean.

Keywords: Marine caves, biodiversity, Eastern Mediterranean, Aegean Sea, Levantine, Marine Strategy Framework Directive.

Introduction

Marine caves constitute a typical feature of the Mediterranean rocky coastline. According to the most recent census, 738 marine caves have been recorded in the eastern Mediterranean to date, representing one fourth of the known Mediterranean marine caves (Giakoumi *et al*., 2013). However, information regarding their biodiversity and community structure is limited compared to their north-western and central Mediterranean counterparts (Gerovasileiou & Voultsiadou, 2014).

The first scientific data concerning the biota of eastern Mediterranean marine caves were acquired during the "CALYPSO" expedition in the 1950s to Kastelorizo, a Greek island in the Levantine Basin (Laborel, 1961; Vacelet, 1961). Later on, Riedl (1966) provided additional biodiversity data for Aegean caves, while scattered information, focusing mainly on the description of rare and new species, was published in more general faunistic and taxonomic studies from the same area (e.g. Bailey, 1969; Hayward, 1974; Pulitzer-Finali & Pronzato, 1981; Pulitzer-Finali, 1983; Voultsiadou-Koukoura & van Soest, 1991; Voultsiadou-Koukoura *et al*., 1991; Voultsiadou & Vafidis, 2004).

Only a limited number of studies concern marine cave biodiversity in the Levantine Basin (e.g. Tsurnamal, 1969; 1975; Ben-Eliahu & Ten Hove, 1992), mostly including information from the coasts of Lebanon, where a number of new species have been described recently (e.g. Pérez *et al*., 2004; Vacelet *et al*., 2007; Harmelin *et al*., 2009). Additional scattered information on Levantine cave biota is presented in studies on alien species (e.g. Bilecenoğlu & Taškavak, 1999; Bitar *et al*., 2007; Tsiakkiros & Zenetos, 2011; Gewing *et al.*, 2014).

Recently, focused research on the biodiversity and community structure of marine caves in the Aegean Sea has increased our knowledge of this habitat (Gerovasileiou & Voultsiadou, 2012; Gerovasileiou *et al.*, 2012; 2013). Gerovasileiou & Voultsiadou (2012) analysed data obtained from marine cave sponge communities in various Mediter-

ranean areas and showed that sponges exhibit clear biogeographic patterns, thus underlining the need to conserve this habitat across the Mediterranean in order to ensure representativeness. Rastorgueff *et al*. (2014) studied cave mysid populations throughout the northern Mediterranean and revealed contrasting patterns of genetic structuring between the western and eastern parts of the basin, which could be attributed to the presence of phylogeographic breaks. Spatial heterogeneity among and within ecoregions is considered a crucial factor that needs to be taken into account in future conservation plans (Giakoumi *et al*., 2013). However, the lack of scientific data on the biodiversity and community structure of fragmented habitats, such as marine caves, could hamper conservation actions.

Taking into account the high level of individuality of this particular habitat and the need to acquire further knowledge that will ensure its adequate conservation, the aim of this work is to: (i) present new data on the biodiversity of marine caves from the north-eastern Mediterranean, (ii) assess marine cave biodiversity throughout the eastern Mediterranean by combining field data and bibliographic information, and (iii) discuss local patterns and unique features.

Materials and Methods

Since 2009, several marine caves in north-eastern Mediterranean coastal and insular areas were surveyed within the framework of a broader scientific study focusing on the biodiversity of Aegean Sea caves. Sampling was performed through SCUBA diving. Additional qualitative information provided by recreational divers (through web fora and direct communication) was also considered.

Furthermore, the scientific literature concerning marine caves of the Mediterranean Sea was reviewed and all biodiversity data were incorporated into a single database along with ecological and spatial information (see Methods in Gerovasileiou & Voultsiadou, 2012; 2014). In this database, protected species (including those under regulated exploitation) were identified according to OCEANA (2009 and references therein) as well as the Greek national legislative framework (e.g. Presidential Decree 67/1981; Thessalou-Legaki & Legakis, 2005; Katsanevakis *et al*., 2011 and references therein). The marine cave biodiversity list was also checked for the presence of alien species (see Methods in Gerovasileiou *et al*., 2015). The ratio of eastern Mediterranean to total Mediterranean marine cave biodiversity was calculated based on data given in Gerovasileiou & Voultsiadou (2014).

The borders of the eastern Mediterranean were defined according to the European Union's Marine Strategy Framework Directive (MSFD) and encompass the Aegean and Levantine ecoregions as defined by Spalding *et al*. (2007). To facilitate analysis, the eastern Mediterranean was further subdivided into three biogeographic subareas: Northern Aegean (NA), Southern Aegean (SA), and Levantine (LB).

Results

A total of 62 studies, published during the last 55 years, were found to include data on marine cave biota of the eastern Mediterranean; however, only 14 of them focused exclusively on marine caves, the rest being general ecological, faunistic, and taxonomic studies. Most studies (41) concerned the Aegean ecoregion (20 in the north and 16 in the south Aegean seas), while 35 studies concerned marine caves of the Levantine Basin. Furthermore, this study provided new biodiversity data for 23 marine caves and cave systems (sites with numerous neighbouring marine caves and tunnels), mainly from insular areas of the north-eastern Mediterranean (Fig. 1).

The combined field research and literature review resulted in a total of 520 taxa belonging to 34 groups (Table 1), representing 24% of total Mediterranean marine cave biodiversity. Sponges were the dominant group in terms of species number followed by polychaetes, rhodophytes, bivalves, fishes and gastropods (Table 2 and Figure 2). Concerning the spatial variability of cave biota, a higher number of taxa was reported from the entrance and semidark zones (260 and 265 taxa respectively), compared to the dark zone (116) whereas, for 92 taxa, the cave zone was not specified.

The northern Aegean Sea displayed the highest number of taxa (324 taxa, representing 15% of total Mediterranean marine cave diversity), followed by the Levantine Basin (175 taxa, 8%) and the southern Aegean (157 taxa, 7%). The best studied northern Aegean caves, Fara and Agios Vasilios, hosted 200 and 170 taxa respectively while the best studied Levantine caves were those of Selaata, harbouring 57 taxa. The various taxonomic groups were not equally represented among areas. For instance, northern Aegean caves hosted 100% of the Mediterranean cave Echiura and Phoronida, 50% of the Tanaidacea, approximately 30% of Porifera, Anthozoa, Sipuncula, Cephalopoda, Brachiopoda, Echinodermata and Pisces, and 25% of Polychaeta and Scyphozoa. Respectively, Levantine caves harboured 50% of the Mediterranean cave Bivalvia and 44% of Brachiopoda, while southern Aegean caves hosted 51% of the Mediterranean marine cave Phaeophyceae and 30% of Rhodophyta.

A considerable proportion of taxa recorded in this study are new records for the marine cave biodiversity of the northern Aegean Sea (55.5%), the southern Aegean Sea (25%), and the Levantine Basin (7%). Additionally, 15 species are reported for the first time in marine caves, either as cave-dwellers or occasional visitors (Table 1). A high number of species (88) are protected by national and international legislation (including those under regulated exploitation) (Table 1). It is notable that 46 alien species (Table 1) have been recorded in caves of the eastern basin, covering 9% of its marine cave biodiversity. Most alien species were recorded in the Levantine Basin (43), covering 25% of local marine cave biodiversity (100% of the recorded Tunicata and Echinodermata, 75% of Bryozoa,

Fig. 1: Map showing the locations of marine caves for which new data are presented in this study (names of caves are given in the Footnote to Table 1).

67% of Gastropoda, 43% of Pisces, 37% of Hydrozoa, 33% of Decapoda, 28% of Polychaeta and 18% of Bivalvia).

The species encountered in several different marine caves in the eastern Mediterranean were: the chlorophyte *Palmophyllum crassum*; the benthic foraminiferan *Miniacina miniacea*; the sponges *Agelas oroides*, *Spirastrella cunctatrix*, *Phorbas tenacior*, *Axinella damicornis*, *Petrosia ficiformis*, *Chondrosia reniformis*, *Ircinia oros*, *Terpios gelatinosa*, *Axinella verrucosa*, and *Dendroxea lenis*; the anthozoans *Madracis pharensis* and *Leptopsammia pruvoti*; the brachiopod *Novocrania anomala*; the tunicate *Halocynthia papillosa*; and the cardinal fish *Apogon imberbis* (Table 1).

Discussion

The limited research effort carried out in the marine caves of the eastern Mediterranean, compared to that of the western Mediterranean, is illustrated by the average trend of cave-related publications: approximately 1 study per year for the eastern basin, versus an upward general trend of 5 studies per year for the entire Mediterranean (Gerovasileiou & Voultsiadou, 2012; 2014). A zoogeographical gradient, i.e. a north-west to south-east decrease of species number was observed for sponges, anthozoans, and polychaetes, in accordance with previous studies (Vafidis *et al*., 1994; Voultsiadou, 2005a; 2009; Gerovasileiou & Voultsiadou, 2012). However, it should be taken into account that geographical patterns of species number generally follow trends in sampling effort and scientific expertise, whereas quantitative information only exists for two marine caves of the northern Aegean Sea (Gerovasileiou *et al*., 2013; 2014).

The studied eastern Mediterranean cave communities present certain differences from their western Mediterranean counterparts, such as (i) a scarcity or lack of erect, branching anthozoans (e.g. gorgonian and red coral facies), which often thrive at the entrance and in semidark zones of north-western Mediterranean caves, and (ii) the presence of species endemic to the eastern Mediterranean. This might be related to temperature and trophic differences between the two basins, as suggested by Bibiloni & Gili (1982) and Uriz *et al*. (1993), who compared marine caves of the Balearic Islands (characterized by oligotrophic conditions and higher water temperatures) and the continental north-western Mediterranean coast. Specific characteristics of marine cave communities from the different areas of the eastern Mediterranean are discussed in detail below.

As indicated by the results, the Aegean Sea is the most thoroughly studied area in the eastern Mediterranean regarding its marine cave biodiversity, and hosts some of the richest caves, as far as species number is concerned, studied in the Mediterranean Sea. However, there are marked differences between its northern and southern sectors the northern Aegean is influenced by the brackish cold water input from the Black Sea through the Dardanelles Strait and higher river runoff in contrast to the southern sector, which receives saline warm water flowing northwards from the Levantine (Lykousis *et al*., 2002). These differences are reflected in the higher productivity and diversity of the northern Aegean (Voultsiadou, 2005a; 2009). In further support of this, Gerovasileiou & Voultsiadou (2012) showed that species composition of the marine cave sponge fauna of the northern Aegean resembled that of the north-western Mediterranean, while the southern Aegean cave sponge fauna displayed closer affinities to that of the Levantine.

In this study, the well-studied northern Aegean marine caves were found to support a rich fauna of sponges, scleractinians, polychaetes, decapods, echinoderms, and fishes, comparable in species number to that of the well-studied north-western Mediterranean caves. They also host endemic eastern Mediterranean species (e.g. the sponges *Axinella cannabina*, *Coscinoderma sporadense*, *Hemiasterella aristoteliana*, and *Ircinia paucifilamentosa*, and the bryozoan *Hippaliosina depressa*), as well as species that are not as common in the north-western basin (e.g. *Madracis pharensis*). The fact that several species found in northern Aegean caves are reported for the first time as cave-dwellers may partly be attributed to the recently increased research effort, but may also reflect the presence of occasional visitors. The scleractinian coral *Ceratotrochus magnaghii* observed on the ceiling of the dark interior zone in two marine caves (10-30 m) is reported for the second time from the eastern Mediterranean. Its present finding in the Aegean Sea constitutes the shallowest record for the species after its recent finding in deep (426-1334 m) *Neopycnodonte-Desmophyllum* framestones, west of Crete (Taviani *et al*., 2011).

Table 1. List of taxa recorded in marine caves of the eastern Mediterranean Sea (NA: Northern Aegean, SA: Southern Aegean, LB: Levantine; CE: cave entrance, SD: semidark zone; D: dark zone, Un: unspecified; † first record as cave-dwellers/occasional visitors, * first record for local marine cave biodiversity, ‡ alien species, ** threatened species or protected by national/international legislation). Numbers represent different marine caves (see Footnote).

Species	NA	SA	LB	Number of caves	Cave zone
Kingdom **Chromista**					
Phylum **Ochrophyta**					
Cladostephus spongiosus (Hudson) C. Agardh		14		1	CE
Cutleria chilosa (Falkenberg) P.C.Silva		14		1	CE
Cystoseira amentacea var. stricta Montagne **		15		1	CE
Cystoseira crinita Duby		15		1	CE
Cystoseira spinosa Sauvageau **		15		1	CE
Dictyopteris polypodioides (De Candolle) J.V. Lamouroux		14		1	CE
Dictyota dichotoma (Hudson) J.V. Lamouroux	1*	15, 16		3	CE
Dictyota implexa (Desfontaines) J.V.Lamouroux		15		1	CE
Halopteris filicina (Grateloup) Kützing		14		1	CE
Hincksia sandriana (Zanardini) P.C.Silva		14		1	CE
Lobophora variegata (J.V. Lamouroux) Womersley ex E.C.Oliveira		14		1	CE
Nereia filiformis (J.Agardh) Zanardini		14		1	CE
Padina pavonica (Linnaeus) Thivy	1*	15		2	CE
Sargassum acinarium (Linnaeus) Setchell **		15		1	CE
Sphacelaria cirrosa (Roth) C. Agardh		14		1	CE
Taonia atomaria (Woodward) J. Agardh		14		1	CE
Zanardinia typus (Nardo) P.C.Silva	1*			1	CE
Zonaria tournefortii (J.V.Lamouroux) Montagne		14		1	CE
Phylum **Foraminifera**					
Miniacina miniacea (Pallas, 1766)	1, 2, 3, 4*	16, 17, 18, 19, 20*		9	CE, SD, D
Kingdom **Plantae**					
Phylum **Chlorophyta**					
Bryopsis duplex De Notaris		15		1	CE
Bryopsis plumosa (Hudson) C. Agardh		15		1	CE
Cladophora echinus (Biasoletto) Kützing		14		1	CE
Codium bursa (Olivi) C.Agardh	2, 4*			2	CE
Flabellia petiolata (Turra) Nizamuddin	1, 2, 4*			3	CE
Palmophyllum crassum (Naccari) Rabenhorst	1, 2, 3, 4	16, 17, 18, 19, 20, 21, 22, 23*	40*	13	CE, SD
Valonia macrophysa Kützing	1, 3*	14, 24		4	CE
Phylum **Rhodophyta**					
Acrodiscus vidovichii (Meneghini) Zanardini		14		1	CE
Aglaothamnion caudatum (J. Agardh) Feldmann-Mazoyer		14		1	CE
Amphiroa cryptarthrodia Zanardini		14		1	CE
Apoglossum ruscifolium (Turner) J. Agardh		14		1	CE
Asparagopsis taxiformis (Delile) Trevisan de Saint-Léon ‡		25		1	CE
Chrysymenia ventricosa (J.V. Lamouroux) J. Agardh		14		1	CE
Corallina sp.			41	1	CE
Crouania attenuata (C. Agardh) J. Agardh		14		1	CE
Cryptonemia lomation (Bertoloni) J. Agardh		14		1	CE
Digenea simplex (Wulfen) C. Agardh		14		1	CE
Dipterosiphonia rigens (Shousboe ex C.Agardh) Falkenberg		14		1	CE
Eupogodon planus (C.Agardh) Kützing		14		1	CE
Feldmannophycus rayssiae (Feldmann & G.Feldmann) Augier & Boudouresque		14		1	CE
Gelidium bipectinatum Furnari		14		1	CE
Gelidium pusillum (Stackhouse) Le Jolis		14		1	CE

(continued)

Table 1 *(continued)*

Species	NA	SA	LB	Number of caves	Cave zone
Gymnothamnion elegans (Schousboe ex C. Agardh) J. Agardh		14		1	CE
Herposiphonia tenella (C.Agardh) Ambronn		14		1	CE
Hydrolithon farinosum (J.V.Lamouroux) D. Penrose & Y.M.Chamberlain		14		1	CE
Hypoglossum hypoglossoides (Stackhouse) F.S.Collins & Hervey		14		1	CE
Irvinea boergesenii (Feldmann) R.J.Wilkes, L.M.McIvor & Guiry		14		1	CE
Jania adhaerens J.V.Lamouroux		14		1	CE
Jania rubens (Linnaeus) J.V.Lamouroux		15		1	CE
Jania virgata (Zanardini) Montagne		14		1	CE
Laurencia obtusa (Hudson) J.V. Lamouroux		15		1	CE
Lithophyllum byssoides (J.V. Lamouroux) Foslie **		15, 26		2	CE
Lithophyllum incrustans R.A.Philippi		26		1	CE
Lithophyllum stictaeforme (Areschoug) Hauck		20*	42	2	CE
Mesophyllum alternans (Foslie) Cabioch & M.L.Mendoza **		20*	40, 42	3	CE
Mesophyllum expansum (Philippi) Cabioch & M.L.Mendoza **	5	14, 26		3	CE
Mesophyllum lichenoides (J.Ellis) M.Lemoine		26		1	CE
Monosporus pedicellatus (J.E.Smith) Solier		14		1	CE
Myriogramme distromatica J.J.Rodríguez ex Boudouresque		14		1	CE
Neogoniolithon mamillosum (Hauck) Setchell & L.R.Mason **		26		1	CE
Neurocaulon foliosum (Meneghini) Zanardini		14		1	CE
Nitophyllum punctatum (Stackhouse) Greville		14		1	CE
Osmundea pinnatifida (Hudson) Stackhouse		15		1	CE
Parviphycus pannosus (Feldmann) G.Furnari		14		1	CE
Peyssonnelia bornetii Boudouresque & Denizot		14, 20		2	CE
Peyssonnelia crispata Boudouresque & Denizot		14		1	CE
Peyssonnelia orientalis (Weber-van Bosse) Cormaci & G.Furnari		14		1	CE
Peyssonnelia rosa-marina Boudouresque & Denizot **	2, 3, 6			3	CE
Peyssonnelia rubra (Greville) J. Agardh		14, 20		2	CE
Peyssonnelia sp.	4		42, 43	3	CE
Peyssonnelia squamaria (S.G.Gmelin) Decaisne		14		1	CE
Phyllophora crispa (Hudson) P.S.Dixon **		14		1	CE
Pleonosporium borreri (Smith) Nägeli		14		1	CE
Pterocladiella capillacea (S.G.Gmelin) Santelices & Hommersand		15		1	CE
Pterocladiella sp.			41	1	CE
Pterothamnion plumula (J.Ellis) Nägeli		14		1	CE
Ptilothamnion pluma (Dillwyn) Thuret		14		1	CE
Radicilingua reptans (Kylin) Papenfuss		14		1	CE
Rhodophyllis divaricata (Stackhouse) Papenfuss		14		1	CE
Rhodymenia ardissonei (Kuntze) Feldmann		14		1	CE
Schizymenia dubyi (Chauvin ex Duby) J.Agardh **		26		1	CE
Sphaerococcus coronopifolius Stackhouse		14		1	CE
Kingdom **Animalia**					
Phylum **Porifera**					
Aaptos aaptos (Schmidt, 1864)	2, 3, 7			3	CE, SD
Acanthella acuta Schmidt, 1862	1, 2, 3, 7, 8	17, 18	46	8	CE, SD, D
Agelas oroides (Schmidt, 1864)	1, 2, 3, 4, 6, 7, 8, 9, 10	16, 17, 18, 19, 20, 22, 23, 24, 27, 28, 29, 30, 31, 32	40, 42	25	CE, SD, D
Aplysilla rosea (Barrois, 1876)	1, 2, 3, 6, 7, 10	24	40*	8	CE, SD, D
Aplysina aerophoba Nardo, 1843 **	3			1	CE, SD, D
Axinella cannabina (Esper, 1794) **	2, 6, 9			3	CE, SD
Axinella damicornis (Esper, 1794)	1, 2, 3, 4, 6	16, 17, 18, 20, 22, 24, 27, 29, 30	40*	15	CE, SD

(continued)

Table 1 *(continued)*

Species	NA	SA	LB	Number of caves	Cave zone
Axinella polypoides Schmidt, 1862 **	8		46, 47, 48	4	SD
Axinella sp.	2, 3			2	SD
Axinella verrucosa (Esper, 1794)	1, 2, 8	22, 23, 24, 28, 30	40*	9	SD
Bubaris sp.	2			1	SD
Cacospongia mollior Schmidt, 1862	7			1	SD
Chondrosia reniformis Nardo, 1847	1, 2, 3, 4, 7, 10	16, 17, 18, 19, 31	42	12	CE, SD, D
Cinachyrella levantinensis Vacelet, Bitar, Carteron, Zibrowius & Perez, 2007			47, 49	2	SD
Clathrina clathrus (Schmidt, 1864)	2, 3	20*	45	4	CE, SD, D
Clathrina coriacea (Montagu, 1814)			45	1	CE, SD
Cliona celata Grant, 1826	2, 8			2	CE, SD
Cliona schmidtii (Ridley, 1881)	1, 2, 3	17, 22	50	6	CE, SD
Cliona viridis (Schmidt, 1862)	2*	33		2	CE, SD
Coscinoderma sporadense Voultsiadou-Koukoura, van Soest & Koukouras, 1991	2, 3, 4, 8			4	SD
Crambe crambe (Schmidt, 1862)	6, 7, 8, 10	16, 18, 34	46	8	CE, SD
Crella sp.	3			1	SD
Dendrilla sp.	2, 3			2	SD, D
Dendroxea lenis (Topsent, 1892)	2, 3, 4	18, 19, 20, 22, 27*	40*	9	CE, SD, D
Didiscus stylifer Tsurnamal, 1969			45	1	CE, SD
Dictyonella incisa (Schmidt, 1880)	1, 2, 3, 7	22*		5	SD
Dictyonella marsilii (Topsent, 1893)	8			1	SD
Dictyonella obtusa (Schmidt, 1862)	3			1	SD
Diplastrella bistellata (Schmidt, 1862)	2, 4, 8	20*		4	SD, D
Diplastrella ornata Rützler & Sará, 1962		33	45	2	D
Discodermia polymorpha Pisera & Vacelet, 2011	8			1	SD
Dysidea avara (Schmidt, 1862)	2			1	SD, D
Dysidea fragilis (Montagu, 1818)	2			1	SD
Erylus discophorus (Schmidt, 1862)	8	33	51	3	SD
Eurypon clavatum (Bowerbank, 1866)	2, 3			2	SD, D
Eurypon sp.	3			1	D
Euryspongia raouchensis Vacelet, Bitar, Carteron, Zibrowius & Perez, 2007			41	1	SD, D
Fasciospongia cavernosa (Schmidt, 1862)	1, 3, 8	17, 20, 22, 24		7	CE, SD
Gastrophanella phoeniciensis Perez, Vacelet, Bitar & Zibrowius, 2004			51	1	D
Geodia cydonium (Jameson, 1811) **	7	33		2	SD
Halichondria sp.1	3			1	SD
Halichondria sp.2	7			1	CE
Halichondrida sp.	2, 3			2	SD, D
Haliclona (Gellius) microsigma (Babic, 1922)	2			1	D
Haliclona (Halichoclona) fulva (Topsent, 1893)	2, 3	24		3	CE, SD, D
Haliclona (Halichoclona) perlucida (Griessinger, 1971)	2			1	SD
Haliclona (Reniera) cratera (Schmidt, 1862)		33		1	Un
Haliclona (Reniera) mediterranea Griessinger, 1971	2			1	CE
Haliclona (Soestella) mucosa (Griessinger, 1971)	1, 2, 3	16, 19, 20, 22		7	CE, SD, D
Haliclona sp.1	1			1	SD, D
Haliclona sp.2	2			1	SD
Haliclona sp.3	2			1	D
Haliclona sp.4	1			1	SD, D
Hamigera hamigera (Schmidt, 1862)			42	1	SD
Hemiasterella aristoteliana Voultsiadou-Koukoura & Van Soest, 1991	8			1	SD

(continued)

Table 1 *(continued)*

Species	NA	SA	LB	Number of caves	Cave zone
Hemimycale columella (Bowerbank, 1874)		16*		1	CE, SD
Hexadella sp.	2, 3			2	SD, D
Hexadella pruvoti Topsent, 1896	1, 2, 3, 4	18, 20, 30		7	CE, SD, D
Hexadella racovitzai Topsent, 1896	2, 3			2	CE, SD, D
Hyrtios collectrix (Schulze, 1880)	2			1	CE
Ircinia dendroides (Schmidt, 1862)		33		1	SD
Ircinia oros (Schmidt, 1864)	1, 2, 4, 6, 7, 10	16, 18, 19, 20, 29		11	CE, SD
Ircinia paucifilamentosa Vacelet, 1961	1, 2, 3, 4, 8		42	6	CE, SD, D
Ircinia variabilis (Schmidt, 1862)	1, 2, 7, 8, 10	18, 24	48	8	CE, SD
Jaspis johnstonii (Schmidt, 1862)	1, 2, 3, 7, 8	17, 18	46	8	CE, SD
Jaspis sp.	3			1	D
Leucetta solida (Schmidt, 1862)			45	1	D
Merlia normani Kirkpatrick, 1908		33	42	2	SD
Microscleroderma lamina Perez, Vacelet, Bitar & Zibrowius, 2004			51	1	D
Myrmekioderma spelaeum (Pulitzer-Finali, 1983)	1, 2, 8	18, 19, 20	46, 48	8	SD, D
Lithistida sp.	1*			1	SD
Oceanapia sp.	2			1	SD
Oscarella balibaloi Pérez, Ivanisevic, Dubois, Pedel, Thomas, Tokina & Ereskovsky, 2011	2, 3			2	CE, SD
Oscarella lobularis (Schmidt, 1862)	4, 8	30*		3	CE, SD
Oscarella microlobata Muricy, Boury-Esnault, Bézac & Vacelet, 1996	2		50	2	D
Oscarella tuberculata (Schmidt, 1868)	2, 3			2	CE, SD
Penares euastrum (Schmidt, 1868)	2, 3, 8	20*	47	5	CE, SD, D
Penares helleri (Schmidt, 1864)	2, 8		46	3	SD
Petrobiona massiliana Vacelet & Lévi, 1958 **		31		1	SD
Petrosia (Petrosia) ficiformis (Poiret, 1789) **	1, 2, 4, 5, 7, 8, 10	18, 20, 22, 24, 27, 33, 34	42	15	CE, SD, D
Petrosia (Strongylophora) vansoesti Boury-Esnault, Pansini & Uriz, 1994	1, 8			2	SD, D
Petrosia pulitzeri Pansini, 1996		33		1	Un
Phorbas tenacior (Topsent, 1925)	1, 2, 3, 4, 6, 7, 8, 10	16, 17, 18, 19, 24, 28, 30, 33	40*	17	CE, SD
Phorbas topsenti Vacelet & Perez, 2008	3	17		2	CE
Placospongia decorticans (Hanitsch, 1895)			48	1	Un
Plakina bowerbanki (Sarà, 1960)	2, 3			2	CE, SD, D
Plakina monolopha Schulze, 1880	3, 8			2	SD, D
Plakina reducta (Pulitzer-Finali, 1983)			46, 48	2	Un
Plakina sp.1	2, 3			2	SD, D
Plakina trilopha Schulze, 1880	3			1	CE, SD, D
Plakina weinbergi Muricy, Boury-Esnault, Bézac & Vacelet, 1998		19	52, 53	3	Un
Plakinastrella copiosa Schulze, 1880	8			1	SD
Plakinidae sp.1	2			1	D
Plakortis simplex Schulze, 1880			51	2	Un
Pleraplysilla spinifera (Schulze, 1879)	1, 2, 3, 10	16, 22		6	CE, SD
Protosuberites rugosus (Topsent, 1893)	2			1	D
Pseudocorticium jarrei Boury-Esnault, Muricy, Gallissian & Vacelet, 1995	2, 3	18*	53	4	CE, SD, D
Raspaciona aculeata (Johnston, 1842)	2, 3*			3	CE, SD

(continued)

Table 1 *(continued)*

Species	NA	SA	LB	Number of caves	Cave zone
Sarcotragus foetidus Schmidt, 1862 **	1, 2, 3, 8, 10			5	CE, SD
Sarcotragus spinosulus Schmidt, 1862	7			1	SD
Spirastrella cunctatrix Schmidt, 1868	1, 2, 3, 4, 5, 6, 7, 9, 10	16, 17, 18, 19, 20, 22, 23, 24, 27, 28, 29, 30, 32, 33	40, 42	25	CE, SD, D
Spongia (Spongia) nitens (Schmidt, 1862)	2, 3			2	SD
Spongia (Spongia) officinalis Linnaeus, 1759 **	1, 2, 7			3	CE, SD
Spongia (Spongia) virgultosa (Schmidt, 1868)	2, 3			2	CE, SD, D
Spongionella pulchella (Sowerby, 1804)	2			1	SD
Spongosorites sp.1	2			1	CE, SD
Stryphnus mucronatus (Schmidt, 1868)	4			1	SD
Sycon elegans (Bowerbank, 1845)	3*			1	SD, D
Sycon humboldti Risso, 1826			45	1	D
Terpios gelatinosa (Bowerbank, 1866)	1, 2, 3, 4, 6, 7, 10	16, 17, 23, 24		11	CE, SD, D
Tethya aurantium (Pallas, 1766) **	2			1	CE
Thymosiopsis cuticulatus Vacelet & Perez, 1998	1, 2, 4, 6	17, 18, 19, 20		8	CE, SD, D
Timea geministellata Pulitzer-Finali, 1978	7			1	CE
Timea sp.1	3			1	D
Timea unistellata (Topsent, 1892)	2, 3	22*		3	CE, SD, D
Topsentia lacazei (Schmidt, 1868)			45	1	D
Phylum **Cnidaria**					
Actinia equina (Linnaeus, 1758)	10*		40*	2	CE, SD
Actinia prasina Gosse, 1860 †	7*			1	SD
Aglaophenia octodonta Heller, 1868			54	1	CE
Aglaophenia picardi Svoboda, 1979			54	1	CE
Bimeria vestita Wright, 1859			54	1	CE
Calliactis parasitica (Couch, 1842)	1*	29, 35		3	SD
Campanularia hincksii Alder, 1856			54	1	CE
Caryophyllia inornata (Duncan, 1878) **	2, 3, 4, 6*	16, 18, 24, 36		8	CE, SD, D
Ceratotrochus magnaghii Cecchini, 1914 **	2, 3*			2	D
Cerianthus membranaceus (Spallanzani, 1784)	2, 5	23, 30, 34		5	CE, SD, D
Cladocora caespitosa (Linnaeus, 1758) **	9			1	Un
Clytia gracilis (Sars, 1850)			54	1	CE
Clytia hemisphaerica (Linnaeus, 1767)			54	1	CE
Clytia linearis (Thorneley, 1900) ‡			54	1	CE
Corallium rubrum (Linnaeus, 1758) **	11			1	CE, SD
Dynamena quadridentata (Ellis & Solander, 1786) ‡			54	1	CE
Eudendrium carneum Clarke, 1882 ‡			54	1	CE
Eudendrium merulum Watson, 1985 ‡			54	1	CE
Eudendrium racemosum (Cavolini, 1785)			54	1	CE
Eudendrium sp.	2, 3			2	CE
Filellum serratum (Clarke, 1879) ‡			54	1	CE
Guynia annulata Duncan, 1872 **		36		1	D
Halopteris diaphana (Heller, 1868) **			54	1	CE
Hoplangia durotrix Gosse, 1860	1, 2, 3, 6	36	55	6	CE, SD, D
Laomedea sp.			54	1	CE
Lafoeina tenuis Sars, 1874			54	1	CE
Leptopsammia pruvoti Lacaze-Duthiers, 1897 **	1, 2, 3, 4	18, 20, 21, 22, 23, 24, 27, 29, 31*	40*	14	CE, SD, D

(continued)

Table 1 *(continued)*

Species	NA	SA	LB	Number of caves	Cave zone
Madracis pharensis (Heller, 1868) **	1, 2, 3, 4, 6, 10	16, 20, 22, 24, 27, 28, 30, 31, 32*	40, 42, 47	18	CE, SD, D
Obelia dichotoma (Linnaeus, 1758)			54	1	CE
Oculina patagonica de Angelis 1908 ‡ **		25	54	1	CE, SD
Paracyathus pulchellus (Philippi, 1842) **	2, 3*	20*		3	SD, D
Parazoanthus axinellae (Schmidt, 1862) **	5, 9	16, 21, 24, 28*	40*	7	SD
Pennaria disticha (Goldfuss, 1820)			54	1	CE
Phyllangia americana mouchezii (Lacaze-Duthiers, 1897) **	2*	24*	55	3	CE, SD, D
Polycyathus muellerae (Abel, 1959) **	1, 2, 4, 6*		40, 55	6	SD, D
Rhizostoma pulmo (Macri, 1778) †	1*			1	SD
Sertularia marginata (Kirchenpauer, 1864) ‡			54	1	CE
Sertularia tongensis (Stechow, 1919) ‡			54	1	CE
Phylum **Ctenophora**					
Ctenophora spp.	1*			1	SD
Phylum **Platyhelminthes**					
Stylochus sp.	2			1	SD
Phylum **Nemertea**					
Nemertea spp.	2, 3*			2	SD, D
Phylum **Nematoda**					
Nematoda spp.	2, 3*			2	SD, D
Phylum **Arthropoda**					
Subphylum **Crustacea**					
Anomura sp.1	2, 3*			2	SD
Athanas nitescens (Leach, 1814)	2, 3*			2	SD
Carupa tenuipes Dana, 1852 ‡		37		1	Un
Charybdis (Charybdis) hellerii (A. Milne-Edwards, 1867) ‡			54	1	SD
Chthamalus sp.	1, 10*			2	CE, SD
Colomastix pusilla Grube, 1861	2, 3*			2	CE, SD, D
Copepoda sp.1	3*			1	SD
Copepoda sp.2	3*			1	SD
Cumacea sp.	2, 3*			2	SD, D
Dardanus arrosor (Herbst, 1796)		35		1	Un
Dardanus calidus (Risso, 1827)	1*	29*		2	SD
Dromia personata (Linnaeus, 1758)	2*	18*		2	D
Eualus occultus (Lebour, 1936)	2, 3*			2	SD
Eurynome aspera (Pennant, 1777)	2*			1	CE
Galathea strigosa (Linnaeus, 1761)	2			1	SD
Gammarus subtypicus Stock, 1966 †	3*			1	SD
Gnathia vorax (Lucas, 1849)	2*			1	CE, SD, D
Hemimysis margalefi sensu lato Alcaraz, Riera & Gili, 1986		18, 19, 38	56	4	Un
Herbstia condyliata (Fabricius, 1787)	2, 3*			2	CE, SD
Janira maculosa Leach, 1814	2, 3*			2	CE, SD, D
Leptocheirus bispinosus Norman, 1908	2, 3*			2	SD, D
Leptochelia savignyi (Kroyer, 1842)	2, 3*			2	SD, D
Leucothoe spinicarpa (Abildgaard, 1789)	2, 3*			2	SD, D
Liljeborgia dellavallei Stebbing, 1906	2, 3*			2	CE, SD
Lysianassa caesarea Ruffo, 1987	2*			1	CE, SD
Mysida spp.	1, 2, 3, 4, 7*			5	SD, D
Palaemon serratus (Pennant, 1777) **	1, 4, 7*			3	SD, D
Palinurus elephas (Fabricius, 1787) **	1, 2, 3*		42	4	CE, SD, D
Paradoxapseudes intermedius (Hansen, 1895) †	2, 3*			2	SD, D

(continued)

Table 1 *(continued)*

Species	NA	SA	LB	Number of caves	Cave zone
Phtisica marina Slabber, 1769	3*			1	SD
Pilumnus minutus De Haan, 1835 ‡	2			1	CE
Plesionika narval (Fabricius, 1787)	2, 3	24, 31*		4	D
Scyllarides latus (Latreille, 1802) **	2*	29*	42	3	D
Scyllarus arctus (Linnaeus, 1758) **	3*			1	D
Stenopus spinosus Risso, 1826	2, 3, 7			3	SD, D
Stenothoe sp.	3*			1	SD
Tanais dulongii (Audouin, 1826)	2*			1	D
Phylum **Annelida**					
Class **Polychaeta**					
Amphiglena mediterranea (Leydig, 1851)	2*			1	SD
Amphinome sp.	3*			1	CE
Amphitrite sp.	2*			1	CE
Boccardia polybranchia (Haswell, 1885) †	2, 3*			2	SD, D
Branchiomma bombyx (Dalyell, 1853)	3*			1	SD
Branchiosyllis exilis (Gravier, 1900)			46, 48, 50	3	Un
Ceratonereis (Composetia) costae (Grube, 1840)	3*			1	SD
Chone collaris Langerhans, 1881	2, 3*			2	SD, D
Chrysopetalum debile (Grube, 1855)	3*			1	SD
Dipolydora armata (Langerhans, 1880)	2*			1	SD
Dodecaceria concharum Örsted, 1843	3*			1	SD
Eupolymnia nebulosa (Montagu, 1818)	2*	16*		2	SD
Eupolymnia nesidensis (Delle Chiaje, 1828)	2*			1	D
Eusyllis kupfferi Langerhans, 1879 ‡			46, 50	2	Un
Exogone (Exogone) naidina Örsted, 1845	2*			1	SD
Exogone sp.	2*			1	CE
Filograna sp.	3*	16, 24*		3	SD
Filogranula annulata (O. G. Costa, 1861)		36		1	Un
Glycera tridactyla Schmarda, 1861 †	2, 3*			2	SD
Harmothoe spinifera (Ehlers, 1864)	2, 3*			2	SD
Hermodice carunculata (Pallas, 1766)	1, 2, 3, 4	17, 20*		6	CE, SD, D
Hydroides heterocerus (Grube, 1868) ‡			45	1	Un
Hydroides minax (Grube, 1878) ‡			45	1	Un
Janua (Dexiospira) pagenstecheri (de Quatrefages, 1865)	5			1	Un
Leodice torquata (Quatrefages, 1866)	2*			1	SD
Lumbrineris funchalensis (Kinberg, 1865)	3*			1	SD
Lysidice ninetta Audouin & Milne-Edwards, 1833	2*			1	SD
Myrianida prolifera (O.F. Müller, 1788)			46	1	Un
Myrianida sp.	3*			1	CE
Neanthes caudata (Delle Chiaje, 1827) †	3*			1	SD
Nereis zonata Malmgren, 1867	2, 3*			2	SD, D
Neodexiospira pseudocorrugata (Bush, 1905)	5			1	Un
Nidificaria clavus (Harris, 1968)	5			1	Un
Notomastus latericeus Sars, 1851	2*			1	SD
Odontosyllis fulgurans (Audouin & Milne Edwards, 1833)			50	1	Un
Oxydromus sp.	3*			1	SD
Palola siciliensis (Grube, 1840)	2*			1	SD
Perinereis sp.	2, 3*			2	CE
Phyllochaetopterus socialis Claparède, 1869	4*			1	D
Phyllodoce sp.	3*			1	CE
Phyllodocidae sp.	2*			1	CE
Pileolaria heteropoma (Zibrowius, 1968)	5			1	Un
Placostegus tridentatus (Fabricius, 1779)	2, 3*			2	SD

(continued)

Table 1 *(continued)*

Species	NA	SA	LB	Number of caves	Cave zone
Platynereis dumerilii (Audouin & Milne Edwards, 1834)	2*			1	SD
Polychaeta sp.	3*			1	CE
Polydora hoplura Claparède, 1869 †	2, 3*			2	SD
Polyophthalmus pictus (Dujardin, 1839)	2*			1	SD
Pontogenia chrysocoma (Baird, 1865)	3*			1	SD
Potamilla torelli (Malmgren, 1866)	2*			1	SD
Prionospio malmgreni Claparède, 1869 †	2*			1	SD
Proceraea aurantiaca (Claparède, 1868)			46	1	Un
Protolaeospira striata (Quievreux, 1963)	5			1	Un
Protula intestinum (Lamarck, 1818)			42	1	SD
Protula tubularia (Montagu, 1803)	2, 3, 4*			3	CE, SD, D
Pseudopotamilla reniformis (Bruguière, 1789)	2, 3*			2	SD, D
Sabella spallanzanii (Gmelin, 1791)	3, 6*	27, 29*		4	CE, SD
Salvatoria sp.	3*			1	CE
Serpula vermicularis Linnaeus, 1767	4*			1	CE, SD
Sphaerosyllis bulbosa Southern, 1914	3*			1	SD
Sphaerosyllis hystrix Claparède, 1863	2, 3*			2	SD
Sphaerosyllis pirifera Claparède, 1868			46, 50	2	Un
Spio filicornis (Müller, 1776)	2*			1	SD
Spiophanes sp.	3*			1	CE
Spirobranchus kraussii (Baird, 1865) ‡			41	1	SD, D
Spirobranchus polytrema (Philippi, 1844)	2, 3*			2	SD
Spirorbis cuneatus Gee, 1964	5			1	Un
Spirorbis sp.	2, 3*			2	CE
Subadyte pellucida (Ehlers, 1864)	3*			1	SD
Syllidia armata Quatrefages, 1866	2*			1	SD
Syllis amica Quatrefages, 1866	2, 3*			2	SD, D
Syllis armillaris (O.F. Müller, 1776)	2*		46, 50	3	SD
Syllis cf. mayeri Musco & Giangrande, 2005 ‡			46, 48	2	Un
Syllis corallicola Verrill, 1900			46, 50	2	Un
Syllis gracilis Grube, 1840	3*		46, 51	3	SD
Syllis hyalina Grube, 1863	2, 3*		46, 50	4	SD
Syllis jorgei San Martín & López, 2000			50	1	Un
Syllis variegata Grube, 1860	2*			1	SD, D
Trypanosyllis zebra (Grube, 1840)			46, 50	2	Un
Vermiliopsis infundibulum (Philippi, 1844)	2*		45	2	SD
Vermiliopsis labiata (O. G. Costa, 1861)	3*			1	SD
Vermiliopsis monodiscus Zibrowius, 1968	2, 3*			2	SD
Vinearia koehleri (Caullery & Mesnil, 1897)	5			1	Un
Phylum **Sipuncula**					
Aspidosiphon (Aspidosiphon) muelleri muelleri Diesing, 1851	2, 3*			2	SD
Phascolosoma (Phascolosoma) granulatum Leuckart, 1828	2*			1	SD
Phylum **Echiura**					
Bonellia viridis Rolando, 1821	2*			1	D
Phylum **Mollusca**					
Acar clathrata (Defrance, 1816)	3*			1	CE
Abra alba (W. Wood, 1802)			46, 48, 58	3	Un
Acteocina mucronata (Philippi, 1849) ‡			46	1	Un
Afrocardium richardi (Audouin, 1826) ‡			46	1	Un
Aplysia dactylomela Rang, 1828 ‡			44	1	Un
Arca noae Linnaeus, 1758 **			58	1	Un
Arcopagia balaustina (Linnaeus, 1758)			58	1	Un
Barbatia barbata (Linnaeus, 1758) **	2*		48	2	CE, SD

(continued)

Table 1 *(continued)*

Species	NA	SA	LB	Number of caves	Cave zone
Berthella aurantiaca (Risso, 1818)			47	1	Un
Bittium reticulatum (da Costa, 1778)	2*			1	SD
Bornia sebetia (O. G. Costa, 1830)			46	1	Un
Brachidontes pharaonis (P. Fischer, 1870) ‡			46, 48, 50, 58	4	Un
Bryopa melitensis (Broderip, 1834) †	2, 3*			2	CE, SD
Cardita calyculata (Linnaeus, 1758)			48, 50	2	Un
Chama asperella Lamarck, 1819 ‡			58	1	Un
Chama gryphoides Linnaeus, 1758	2*			1	SD
Chama pacifica Broderip, 1835 ‡			46, 47, 48, 50, 51, 58	6	Un
Chamelea gallina (Linnaeus, 1758) **			46	1	Un
Charonia variegata (Lamarck, 1816) †**		32*		1	SD
Chelidonura fulvipunctata Baba, 1938 ‡			57	1	Un
Conomurex decorus (Röding, 1798) ‡			54	1	SD
Corbula gibba (Olivi, 1792)			46, 48	2	Un
Coripia corbis (Philippi, 1836)			46	1	Un
Coripia jozinae (Van Aartsen, 1985)			46, 48	2	Un
Ctena decussata (O. G. Costa, 1829)			46, 48, 58	3	Un
Diodora sp.	2, 3*			2	SD, D
Dosinia lupinus (Linnaeus, 1758)			58	1	Un
Eledone moschata (Lamarck, 1798)	9			1	CE
Elysia viridis (Montagu, 1804)	9			1	CE
Felimare picta (Schultz in Philippi, 1836)	3*			1	CE
Flabellina affinis (Gmelin, 1791)	1*			1	CE
Flabellina pedata (Montagu, 1815)		16*		1	SD
Fusinus pulchellus (Philippi, 1844)	12			1	Un
Glans trapezia (Linnaeus, 1767)			46, 48	2	Un
Glycymeris sp. (juveniles of *G. bimaculata* and/or *G. pilosa*)			46	1	Un
Gonilia calliglypta (Dall, 1903)			46	1	Un
Goniobranchus annulatus (Eliot, 1904) ‡			48	1	CE
Goodallia triangularis (Montagu, 1803)			46	1	Un
Gouldia minima (Montagu, 1803)			46, 48	2	Un
Hiatella arctica (Linnaeus, 1767)	2, 3*			2	CE, SD
Hypselodoris infucata (Rüppell & Leuckart, 1830) ‡			54	1	SD, D
Irus irus (Linnaeus, 1758)			58	1	Un
Lima lima (Linnaeus, 1758)			48, 50	2	Un
Lithophaga lithophaga (Linnaeus, 1758) **	2, 3, 4*		46, 47, 48, 50, 58	8	CE, SD, D
Loripes lucinalis (Lamarck, 1818)			46, 58	2	Un
Loripinus fragilis (Philippi, 1836)			46, 48	2	Un
Lucinella divaricata (Linnaeus, 1758)			46	1	Un
Luria lurida (Linnaeus, 1758) **	2*			1	D
Malleus regula (Forsskål in Niebuhr, 1775) ‡			46, 47, 48, 50, 51, 58	6	Un
Manupecten pesfelis (Linnaeus, 1758)	2			1	SD

(continued)

Table 1 *(continued)*

Species	NA	SA	LB	Number of caves	Cave zone
Megaxinus unguiculinus Pallary, 1904			46	1	Un
Mimachlamys varia (Linnaeus, 1758)			46	1	Un
Mitra sp.	2			1	SD
Modiolus barbatus (Linnaeus, 1758) **	3*		48	2	CE
Musculus costulatus (Risso, 1826)			46	1	Un
Musculus subpictus (Cantraine, 1835)			58	1	Un
Neopycnodonte cochlear (Poli, 1795)	2, 3*			2	CE, SD
Nucula nucleus (Linnaeus, 1758)			46, 48, 58	3	Un
Nuculana pella (Linnaeus, 1767)			48	1	Un
Papillicardium papillosum (Poli, 1791)			58	1	Un
Parvicardium scriptum (Bucquoy, Dautzenberg & Dollfus, 1892)			46, 48, 58	3	Un
Peltodoris atromaculata Bergh, 1880	1, 2, 5, 12	20, 21, 34		7	CE, SD
Pinctada imbricata radiata (Leach, 1814) ‡			54	1	SD
Pinna nobilis Linnaeus, 1758 **	2*			1	SD
Pleurobranchus forskalii Rüppell & Leuckart, 1828 ‡			51	1	Un
Pyrunculus fourierii (Audouin, 1826) ‡			58	1	Un
Raphitoma sp.	2*			1	CE
Ringicula auriculata (Ménard de la Groye, 1811)			46, 48, 58	3	Un
Rocellaria dubia Pennant, 1777	2, 3*			2	CE, SD
Sandalia triticea (Lamarck, 1810)	12			1	Un
Semicassis granulata (Born, 1778)			40*	1	Un
Sphenia rueppellii A. Adams, 1851 ‡			47	1	Un
Spisula subtruncata (da Costa, 1778) **			58	1	Un
Spondylus spinosus Schreibers, 1793 ‡			46	1	Un
Striarca lactea (Linnaeus, 1758)			46, 48, 50, 51, 58	5	Un
Thracia phaseolina (Lamarck, 1818)			58	1	Un
Thuridilla hopei (Vérany, 1853)	2*			1	CE
Tylodina perversa (Gmelin, 1791)	3*			1	CE, SD
Umbraculum umbraculum (Lightfoot, 1786)	1*		41	2	CE, SD
Venerupis geographica (Gmelin, 1791) **			46	1	Un
Venus verrucosa Linnaeus, 1758 **			46	1	Un
Vermetidae	3*			1	SD
Phylum **Bryozoa**					
Adeonella pallasii (Heller, 1867)	1, 2, 3*			3	CE, SD
Bugula sp.	1, 2, 3*			3	CE, SD
Crisia sp.	1, 2, 3*			3	CE, SD
Frondipora verrucosa (Lamouroux, 1821)	3*			1	CE, SD
Hippaliosina depressa (Busk, 1854)	1, 2, 3			3	CE, SD, D
Microporella coronata (Audouin, 1826) ‡			50, 51	2	Un
Microporella harmeri Hayward, 1988 ‡			46	1	Un
Myriapora truncata (Pallas, 1766)	3, 5	17, 22, 23, 24*		6	CE, SD
Onychocella marioni (Jullien, 1882)	2			1	D
Parasmittina egyptiaca (Waters, 1909) ‡			46, 47, 50, 51, 58	5	Un

(continued)

Table 1 *(continued)*

Species	NA	SA	LB	Number of caves	Cave zone
Parasmittina raigii (Audouin, 1826)			47	1	Un
Parasmittina serruloides Harmelin, Bitar & Zibrowius, 2009 ‡			46, 51	2	Un
Reteporella sp.	3*	18, 24*	40*	4	CE, SD, D
Reteporellina delicatula Hayward, 1974	5			1	Un
Rhynchozoon neapolitanum Gautier, 1962	2, 3*	23, 24*		4	CE, SD
Schizoretepora hassi Harmelin, Bitar & Zibrowius, 2007 ‡			46, 47, 48, 50, 58	5	SD
Schizomavella sp.	3*			1	CE, SD
Smittina nitidissima (Hincks, 1880) ‡			46, 48, 50	3	Un
Turbicellepora coronopus (Wood, 1844) †	2, 3*			2	CE, SD
Phylum **Brachiopoda**					
Argyrotheca cistellula (Searles-Wood, 1841)			58, 60	2	Un
Argyrotheca cuneata (Risso, 1826)			46, 47, 48, 50, 51, 58, 59, 60	8	Un
Joania cordata (Risso, 1826)	13		46, 47, 48, 51, 58	6	Un
Novocrania anomala (Müller, 1776)	2, 3*	20*	46, 47, 48, 50, 51, 58, 60, 61, 62	12	SD, D
Megathiris detruncata (Gmelin, 1790)	13			1	Un
Phylum **Phoronida**					
Phoronis australis Haswell, 1883 †	2*			1	CE
Phylum **Echinodermata**					
Amphipholis squamata (Delle Chiaje, 1828)	2*			1	D
Arbacia lixula (Linnaeus, 1758)	1, 2, 3, 4, 7, 10*	30*		7	CE, SD, D
Centrostephanus longispinus (Philippi, 1845) **	2, 3	22*		3	CE, SD, D
Hacelia attenuata Gray, 1840 **	1, 2, 3	27*		4	CE, SD
Holothuria (Panningothuria) forskali Delle Chiaje, 1823 **	4*			1	CE, SD
Holothuria (Platyperona) sanctori Delle Chiaje, 1823 **	1, 2, 3*			3	CE, SD, D
Marthasterias glacialis (Linnaeus, 1758)	3*	34		2	CE
Ophidiaster ophidianus (Lamarck, 1816) **	1, 3*			2	CE
Ophiothrix fragilis (Abildgaard, 1789)	1, 2, 3, 4*			4	CE, SD
Peltaster placenta (Müller & Troschel, 1842) †	3*			1	D
Sphaerechinus granularis (de Lamarck, 1816)	3*			1	CE
Synaptula reciprocans (Forskål, 1775) ‡			54	1	SD

(continued)

Table 1 *(continued)*

Species	NA	SA	LB	Number of caves	Cave zone
Phylum **Chordata**					
Subphylum **Tunicata**					
Didemnum sp.	1*			1	CE, SD
Halocynthia papillosa (Linnaeus, 1767) **	2, 3, 4, 6, 9	16, 23, 24, 27*		9	CE, SD
Herdmania momus (Savigny, 1816) ‡			40, 45, 63	3	SD
Microcosmus vulgaris Heller, 1877	2, 3, 6, 9			4	CE, SD
Phallusia nigra Savigny, 1816 ‡			54	1	SD, D
Salpidae	1*			1	SD
Symplegma brakenhielmi (Michaelsen, 1904) ‡			54	1	SD
Tunicata sp.1	3*			1	D
Tunicata sp.2	3*			1	CE, SD
Subphylum **Vertebrata**					
Superclass **Pisces**					
Anthias anthias (Linnaeus, 1758) **	2, 3, 4			3	CE, SD
Apogon (Apogon) imberbis (Linnaeus, 1758) **	1, 2, 3, 4, 5, 7	16, 27*	40*	9	CE, SD, D
Boops boops (Linnaeus, 1758) **	3			1	CE
Bothus podas (Delaroche, 1809) **	2*			1	SD
Chromis chromis (Linnaeus, 1758) **	1, 2, 3	16*		4	CE, SD, D
Conger conger (Linnaeus, 1758) **	1, 3*			2	CE, SD
Coris julis (Linnaeus, 1758) **	1, 3			2	CE, SD
Diplodus annularis (Linnaeus, 1758) **	1*			1	CE, SD
Diplodus sargus sargus (Linnaeus, 1758) **	1, 2, 9			3	CE, SD
Diplodus vulgaris (Geoffroy Saint-Hilaire, 1817) **	1, 2, 4*			3	CE, SD, D
Enchelycore anatina (Lowe, 1838)			51	1	CE
Epinephelus costae (Steindachner, 1878) **	2*			1	D
Epinephelus marginatus (Lowe, 1834) **	2*		42	2	CE
Gobius auratus Risso, 1810 † **	2, 3*			2	CE, SD
Lepadogaster candolii Risso, 1810 **	3*			1	SD
Mugil sp. **	1, 7*			2	CE
Mullus surmuletus Linnaeus, 1758 **	1, 2*			2	CE, SD
Muraena helena Linnaeus, 1758 **	1, 3, 4*			3	CE, SD
Oblada melanura (Linnaeus, 1758) **	1, 7, 9			3	CE, SD
Parablennius gattorugine (Linnaeus, 1758) **	7*			1	CE, SD
Parablennius rouxi (Cocco, 1833) **	2*			1	SD
Pempheris vanicolensis Cuvier, 1831 ‡		39	40, 64, 65	4	CE, SD
Phycis phycis (Linnaeus, 1766) **	2, 3, 7			3	CE, SD, D
Sargocentron rubrum (Forsskål, 1775) ‡		31, 39	40, 64, 66	5	CE, SD
Sarpa salpa (Linnaeus, 1758) **	2*			1	CE
Sciaena umbra Linnaeus, 1758 **	1, 2, 4		42	4	SD, D
Scorpaena maderensis Valenciennes, 1833 **	2*			1	CE, SD
Scorpaena porcus Linnaeus, 1758 **	2, 7*			2	CE, SD
Scorpaena scrofa Linnaeus, 1758 **	3*			1	CE, SD
Seriola dumerili (Risso, 1810) **		29*		1	CE, SD
Serranus cabrilla (Linnaeus, 1758) **	1, 2, 3			3	CE, SD, D
Serranus scriba (Linnaeus, 1758) **	1, 2, 4*			3	CE, SD, D
Siganus luridus (Rüppell, 1829) ‡			40	1	CE
Sparisoma cretense (Linnaeus, 1758) **	1*			1	CE

(continued)

Table 1 *(continued)*

Species	NA	SA	LB	Number of caves	Cave zone
Spicara maena (Linnaeus, 1758) **	3*			1	CE
Symphodus mediterraneus (Linnaeus, 1758) **	1*			1	SD
Tripterygion delaisi Cadenat & Blache, 1970 **	7*			1	CE
Class **Aves**					
Alcedo atthis (Linnaeus, 1758) **	1*			1	
Class **Mammalia**					
Monachus monachus (Hermann, 1779) **	+	+	+		CE, SD, D

Northern Aegean caves

1. Trypia Spilia, Agios Efstratios Island, Greece (Gerovasileiou & Voultsiadou, 2012; this study)
2. Fara Bay Islet, Lesvos Island, Greece (Gerovasileiou *et al*., 2009; 2012; 2013; Gerovasileiou & Voultsiadou, 2012; this study)
3. Agios Vasilios Islet, Lesvos Island, Greece (Gerovasileiou *et al*., 2009; 2012; 2014; Gerovasileiou & Voultsiadou, 2012; this study)
4. Cape Drepanon, Chalkidiki Peninsula, Greece (Voultsiadou-Koukoura & van Soest, 1991; Voultsiadou-Koukoura *et al*., 1991; Voultsiadou-Koukoura & Koukouras, 1993; this study)
5. Emborios cave, Chios Island, Greece (Jones *et al*., 1968; Bailey, 1969; Hayward, 1974)
6. Avlaki, Chalkidiki Peninsula, Greece (this study)
7. Ftelio cave, Agios Efstratios Island, Greece (Gerovasileiou & Voultsiadou, 2012; this study)
8. Youra Island caves, Sporades Islands, Greece (Voultsiadou, 1986; Voultsiadou-Koukoura & van Soest, 1991; Voultsiadou-Koukoura *et al*., 1991; Voultsiadou-Koukoura & Koukouras, 1993; Voultsiadou & Vafidis, 2004; Voultsiadou, 2005b)
9. Marmaras, Chalkidiki Peninsula, Greece (Riedl, 1966)
10. Red caves, Chalkidiki Peninsula, Greece (this study)
11. Northen Aegean Sea, Greece (Dounas *et al*., 2009)
12. Chalkidiki Peninsula, Greece (Antoniadou & Chintiroglou, 2005)
13. Northern Evoikos, Greece (Logan *et al*., 2002)

Southern Aegean caves

14. Sykia cave, Milos Island, Greece (Lazaridou & Charitonidis, 1993)
15. Lindos caves, Rhodes Island, Greece (Tsekos & Haritonidis, 1974)
16. Vouliagmeni pit, Attica, Greece (Gerovasileiou & Voultsiadou, 2012; this study)
17. Madhes cave, Crete, Greece (Gerovasileiou & Voultsiadou, 2012; this study)
18. Alykes cave, Crete, Greece (Gerovasileiou & Voultsiadou, 2012; Rastorgueff *et al*., 2014 as "Blue Cave"; this study)
19. Stavros cave, Crete, Greece (Gerovasileiou & Voultsiadou, 2012; this study)
20. Kalathas cave, Crete, Greece (this study)
21. Amorgos Island, Greece (this study)
22. Fourni Island, Greece (this study)
23. Polyaigos Island, Greece (this study)
24. Andros Island, Greece (Gerovasileiou & Voultsiadou, 2012; this study)
25. Saronikos Gulf, Greece (Salomidi *et al*., 2013)
26. Kallithea caves, Rhodes Island, Greece (Tsekos & Haritonidis, 1974)
27. Syros Island, Greece (this study)
28. Gyaros Island, Greece (this study)
29. Pandieronisi Islet, Cyclades, Greece (this study)
30. Porto Rafti, Attica, Greece (this study)
31. Rhodes Island, Greece (André *et al*., 2009; this study)
32. Kolymbari, Crete, Greece (this study)
33. Gournia, Agios Nikolaos, Crete, Greece (Pulitzer-Finali & Pronzato, 1981; Pulitzer-Finali, 1983; Pansini, 1996)
34. Aegina Island, Greece (Riedl, 1966)
35. Cape Sounion, Greece (Riedl, 1966)
36. Kali Limines, Crete, Greece (Zibrowius, 1968; 1971; 1978; Bitar & Zibrowius, 1997)
37. Dalyan, Muğla, Turkey (Yokes & Galil, 2006)
38. Schinaria Bay, Crete, Greece (Rastorgueff *et al*., 2014)
39. Southern Aegean coasts of Turkey (Bilecenoglu, 2010)

Levantine Sea caves

40. Blue Cave, Kastelorizo Island, Greece (Katsanevakis *et al*., 2014; this study)
41. Raoucheh cave, Lebanon (Zibrowius & Bitar, 2003; Vacelet *et al*., 2007; Bitar, 2010; Crocetta *et al*., 2013b)
42. Cape Greco, Cyprus (Ramos-Esplá *et al*., 2007)
43. Cape Matapan, Kastelorizo Island, Greece (Laborel, 1961; Vacelet, 1961)
44. Saadiyat, Lebanon (Crocetta *et al*., 2013b)
45. Rosh-HaNiqra, Israel (Tsurnamal, 1969; 1975; Ben-Eliahu & Ten Hove, 1992; Gewing *et al*., 2014)
46. Selaata caves, Lebanon (Logan & Long, 2001; Carteron, 2002; Logan *et al*., 2002; Aguado & San Martin, 2007; Harmelin *et al*., 2007; 2009; 2011; Crocetta *et al*., 2013a,b)
47. Kafar Abida, Lebanon (Carteron, 2002; Logan *et al*., 2002; Aguado & San Martin, 2007; Bitar & Zibrowius, 1997; Harmelin *et al*., 2007; Vacelet *et al*., 2007; Harmelin *et al*., 2009; Crocetta *et al*., 2013a,b)
48. Ras El Chakaa, Lebanon (Carteron, 2002; Logan *et al*., 2002; Aguado & San Martin, 2007; Harmelin *et al*., 2007; 2009; Crocetta *et al*., 2013a,b)
49. Sdot Yam, Israel (Meroz-Fine *et al*., 2005)
50. Ramkine Island, Lebanon (Logan & Long, 2001; Carteron, 2002; Logan *et al*., 2002; Aguado & San Martin, 2007; Harmelin *et al*., 2007; 2009; 2011; Crocetta *et al*., 2013a ; Crocetta & Russo, 2013)
51. Chak El Hatab caves, Lebanon (Carteron, 2002; Logan *et al*., 2002; Perez *et al*., 2004; Aguado & San Martin, 2007; Harmelin *et al*., 2007; 2009; 2011; Bitar, 2013; Crocetta *et al*., 2013a,b; Crocetta & Russo, 2013)
52. Cape Arnaoutis, Agios Georgios Island, Cyprus (Muricy *et al*., 1998)
53. Lebanon (Ereskovsky *et al*., 2009)
54. Lebanese caves and tunnels (Bitar *et al*., 2007; Morri *et al*., 2009; Bitar, 2010)
55. Tabarja, Lebanon (Bitar & Zibrowius, 1997)
56. Kas, Turkey (Rastorgueff *et al*., 2014)
57. Cyclops Cave, Protaras, Cyprus (Tsiakkiros & Zenetos, 2011)
58. Jbail – Tablieh cave, Lebanon (Logan & Long, 2001; Logan *et al*., 2002; Harmelin *et al*., 2009; Crocetta *et al*., 2013a,b; Crocetta & Russo, 2013)
59. Termik Santral (east of Keryneia/Girne), Cyprus (Logan *et al*., 2002)
60. Rizokarpason/Dipkarpas, Cyprus (Logan *et al*., 2002)
61. El Kassmieh, Lebanon (Logan & Long, 2001)
62. Cape Shikmona, Haifa, Israel (Logan & Long, 2001)
63. Lebanese caves (Harmelin *et al*., 2007)
64. Levantine and coasts of Turkey (Bilecenoglu, 2010)
65. Antalya Bay, Turkey (Bilecenoglu & Taskavak, 2009)
66. Beirut, Lebanon (Riedl, 1966)

Table 2. Number of taxa per taxonomic group recorded in marine caves of the eastern Mediterranean (NA: Northern Aegean, SA: Southern Aegean, LB: Levantine). The percent contribution of each group to the total Mediterranean marine cave diversity was calculated based on data given in Gerovasileiou & Voultsiadou (2014).

Taxonomic group	NA	SA	LB	Total number of taxa	% contribution to total Mediterranean marine cave diversity
Phaeophyceae	3	17		18	54.5
Foraminifera	1	1		1	7.1
Chlorophyta	4	5	1	7	25.9
Rhodophyta	3	51	5	53	31.4
Porifera	95	42	39	116	36.5
Hydrozoa	1		19	19	17.6
Anthozoa	15	11	8	17	34.7
Scyphozoa	1			1	25
Ctenophora	1			1	100
Platyhelminthes	1			1	2.8
Nemertea	1			1	11.1
Nematoda	1			1	2.7
Copepoda	2			2	1.8
Cirripedia	1			1	14.3
Decapoda	15	6	3	18	24.7
Mysida	1	1	1	1	4.8
Tanaidacea	3			3	50
Isopoda	2			2	13.3
Amphipoda	8			8	9.6
Cumacea	1			1	16.7
Polychaeta	67	5	18	79	30.3
Sipuncula	2			2	33.3
Echiura	1			1	100
Gastropoda	15	3	12	28	20.9
Bivalvia	11		45	53	58.9
Cephalopoda	1			1	33.3
Bryozoa	12	3	8	18	8.2
Brachiopoda	3	1	4	5	55.6
Phoronida	1			1	100
Echinodermata	11	4	1	12	35.3
Tunicata	6	1	3	9	22
Pisces	32	5	7	37	38.5
Aves	1			1	
Mammalia	1	1	1	1	
Total	**324**	**157**	**175**	**520**	**24**

In the rest of the Mediterranean, this anthozoan was found in semidark and dark caves of Marseille (7-37 m) and Croatia (40 m), as well as on coralligenous beds and in deeper waters, down to 400 m (Zibrowius, 1978). Interestingly, along the southern coasts of Crete, 2 rare benthic species were recorded, not yet found in other eastern Mediterranean caves, namely, the polychaete *Filogranula annulata* (Zibrowius, 1968; 1971) and the deep-sea scleractinian *Guynia annulata* reported from a dark cave with freshwater infiltrations (Zibrowius, 1971; 1978).

The detailed study of the macroalgal assemblages in a semi-submerged cave in Milos Island, southern Aegean Sea (Lazaridou & Charitonidis, 1993), yielded 68 species (11 phaeophytes, 6 chlorophytes, and 51 rhodophytes). The majority of the species recorded were sciaphilic (62%), but several photophilic species were also found in well-lit sectors due to the shallow depth and complex cave morphology. The macroalgal diversity within this cave is considered high compared to other well studied Mediterranean caves, where a range of 34-56 macroalgal species per cave have been recorded (e.g. Martí *et al*., 2004; Alongi *et al*., 2012). This fact could possibly be attributed to the cave geomorphology and climatic factors of the southern Aegean resulting in higher levels of sunlight locally. It should be taken into account that there are still major knowledge gaps with regard to Aegean marine flora, and particularly understudied habitats, such as caves, and that future studies are expected to increase the number of species in this region (Tsiamis *et al*., 2013; 2014). Furthermore, the known sponge diversity from southern Aegean marine caves is two times lower than that of the well-studied caves of the more eutrophic northern Aegean Sea. However, *in situ* observations by the authors showed that the cave communities of the southern Aegean islands were richer in sessile biota than those of the adjacent, well-lit infralittoral beds, where sciaphilic species (e.g.

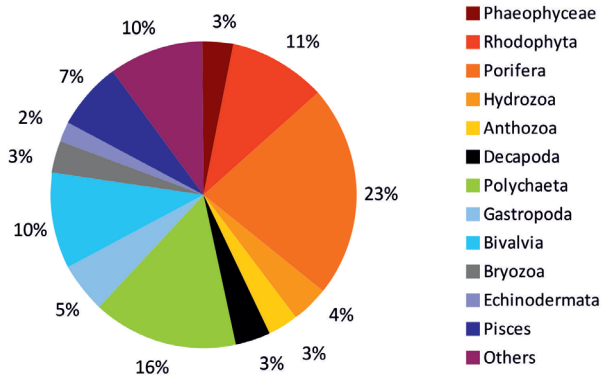

Fig. 2: Taxonomic composition of marine cave biota in the eastern Mediterranean.

rhodophytes, sponges, and anthozoans) were rare or even absent. This fact highlights the significant role of marine caves in the southern Aegean marine ecosystem.

The sponge fauna of the studied Levantine marine caves is characterized by the largest number of endemic and warm-water species in the entire Mediterranean Sea (Gerovasileiou & Voultsiadou, 2012). They host 3 sponge species with a narrow range of distribution, *Cinachyrella levantinensis*, *Euryspongia raouchensis*, and *Gastrophanella phoeniciensis*, which possibly constitute remnants of the thermophilous biota that lived in the Mediterranean Sea during warmer periods and have survived in the warmest part of the Levantine Basin only (Pérez *et al*., 2004; Vacelet *et al*., 2007). A large number of hydrozoans and bivalves have been found in marine caves of the area, possibly reflecting the specific research interests of the experts involved (e.g. Morri *et al*., 2009; Crocetta *et al*., 2013a). The large number of alien species reported from marine caves in this area highlights the need for scientific monitoring.

Conclusive remarks

This overview of eastern Mediterranean marine caves revealed a rich biodiversity, including several protected, endemic, and alien species. However, many taxonomic groups (e.g. macro-algae, hydrozoans, and bryozoans) were inadequately or unevenly studied across different areas. Furthermore, cave biodiversity data are completely lacking for certain eastern and southern areas (e.g. coasts of Turkey, Syria, Egypt, and Libya). The fact that the existing knowledge concerning the marine cave biota of the eastern Mediterranean is far from being complete, and that a moderate research effort yielded several new and alien species, indicates that future surveys are expected to increase the number of cave-dwelling species in this area significantly, including important endemic and alien components.

The high levels of biodiversity and endemism characterizing eastern Mediterranean marine caves highlight the need for protecting these ecosystems. Marine caves constitute fragmented habitats (Harmelin *et al*., 1985), especially in the eastern Mediterranean, an area presenting heterogeneity in abiotic conditions, seascape, and coastline geomorphology. These features may function as phylogeographic breaks, influencing isolation and triggering speciation processes, as shown by Rastorgueff *et al*. (2014). The vast majority of marine caves recorded in the Aegean ecoregion are located in insular areas (Giakoumi *et al*., 2013), possibly indicating a higher level of isolation (Bibiloni *et al*., 1989). However, isolation mechanisms for marine cave assemblages are not always clear and the availability of a large number of caves in this area could facilitate connectivity among cave populations, in so far as caves could be used as 'stepping-stone habitats' (Rastorgueff *et al*., 2014). As connectivity is an important consideration in marine conservation planning, the availability and isolation of these habitats should be considered in future spatial prioritization schemes.

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