

SCIENTIA MARINA 80(4)
December 2016, 553, Barcelona (Spain)
ISSN-L: 0214-8358

Sponges as “living hotels” in Mediterranean marine caves (Erratum)

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Citation/Como citar este artículo: Gerovasileiou V., Chintiroglou C.C., Konstantinou D., Voultziadou E. 2016. Spong-es as “living hotels” in Mediterranean marine caves (Erratum). *Sci. Mar.* 80(4): 553.

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The terms “symbiosis” and “symbiont”, used in parts of the original article (Gerovasileiou et al. 2016), may not disclose the full range of relationships among the sponge and the associated organisms. Thus, it is considered more appropriate to replace them with the terms “association” and “inhabitant” respectively.

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Gerovasileiou V., Chintiroglou C.C., Konstantinou D., Voultziadou E. 2016. Sponges as “living hotels” in Mediterranean marine caves. *Sci. Mar.* 80(3): 279-289. doi: <http://dx.doi.org/10.3989/scimar.04403.14B>

Sponges as “living hotels” in Mediterranean marine caves

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Summary: Although sponges constitute the dominant sessile organisms in marine caves, their functional role as ecosystem engineers has received little attention in this habitat type. In this study the associated macrofauna of the massive/tubular ecosystem-engineering sponges *Agelas oroides* and *Aplysina aerophoba* was studied across distinct ecological zones of two eastern Mediterranean caves. Our results revealed that the examined sponges supported a considerable associated macrofauna. A total of 86 associated taxa were found, including species reported for the first time as sponge symbionts and typical cave dwellers. Crustaceans predominated in terms of abundance but polychaetes showed the highest number of taxa. A clear differentiation was observed in the structure of the associated assemblage between the two sponges, attributed not only to the sponge species but also to differences in the surrounding environment. Density, diversity and the trophic structure of the sponge-associated macrofauna did not vary significantly along the horizontal axis of the surveyed caves. These findings suggest that sponges form a quite stable habitat, maintaining their functional role as ecosystem engineers across the studied marine caves and increasing habitat complexity in the impoverished inner dark cave sectors.

Keywords: Porifera; sponges; marine caves; ecosystem engineers; symbiosis; macrofauna; feeding groups; Mediterranean Sea; Aegean Sea.

Esponjas como “hoteles vivientes” en cuevas submarinas del Mediterráneo

Resumen: A pesar de que las esponjas constituyen el grupo sétil dominante en cuevas submarinas, su papel como ingenieros del ecosistema dentro de estos ambientes ha recibido muy poca atención. En el presente trabajo, se ha estudiado la macrofauna asociada a las especies *Agelas oroides* y *Aplysina aerophoba* (ambas con una morfología masiva-tubular y consideradas como especies ingenieras del ecosistema) a lo largo de diferentes ambientes situados en dos cuevas marinas del Mediterráneo oriental. Nuestros resultados ponen de manifiesto que las dos especies de esponjas consideradas albergan una abundante fauna asociada. Se encontró un total de 86 taxones diferentes, muchos de los cuales son citados por primera vez como simbioses de esponjas y habitantes de cuevas submarinas. Aunque los crustáceos fueron el grupo dominante en términos de abundancia, fueron los poliquetos los que presentaron la mayor riqueza taxonómica. Las comunidades asociadas a una y otra esponja presentaron claras diferencias, lo cual se atribuye no solo a diferencias relacionadas con las especies hospedadoras sino también al ambiente circundante. La densidad, diversidad y estructura trófica de la macrofauna asociada a las esponjas no varió significativamente a lo largo del eje horizontal de las cuevas muestreadas. Estos resultados sugieren que las esponjas forman un hábitat bastante estable, manteniendo su papel funcional como ingenieros del ecosistema a lo largo de las cuevas submarinas y, por tanto, incrementando la complejidad del hábitat en los sectores más internos, empobrecidos y oscuros de las cuevas.

Palabras clave: Porifera; esponjas; cuevas marinas; ingenieros del ecosistema; simbiosis; macrofauna; grupos tróficos; mar Mediterráneo; mar Egeo.

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Editor: M.J. Uriz.

Received: January 11, 2016. **Accepted:** April 22, 2016. **Published:** September 26, 2016

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INTRODUCTION

One of the most important roles of sponges in the marine ecosystem is that they function as ecosystem engineers or “living hotels”, providing micro-habitat to diverse organisms (e.g. Koukouras et al. 1985, Ribeiro et al. 2003, Padua et al. 2013). This ecological role of sponges has gained increasing research interest over the last few decades for both scientific and conservation purposes. Sponge-associated fauna has been studied in a variety of habitats, ranging from shallow rocky beds in temperate seas (Koukouras et al. 1985, 1992, 1996) to tropical coral reefs (Villamizar and Lauchlin 1991), seagrass meadows (Çinar et al. 2002), polar regions (Amsler et al. 2009) and deep-sea ecosystems (Klitgaard 1991).

Although sponges constitute the dominant sessile organisms in marine cave environments (Gerovasileiou and Voultziadou 2012, 2016), their functional role as ecosystem engineers in this habitat type has received little attention. Recently, Navarro-Barranco et al. (2016) studied the crustaceans associated with invertebrate hosts, among which the sponge *Ircinia variabilis*, in a marine cave in the Alboran Sea and found that all the examined species were equally used as refuges by crustaceans.

Sessile assemblages of marine caves are characterized by a decrease in diversity, biomass and three-dimensional complexity towards inner dark cave sectors, driven by the extreme oligotrophy due to the reduction of light and the increasing water confinement (Harmelin et al. 1985, Bianchi and Morri 1994). On the other hand, sessile invertebrates have been shown to increase the structural complexity of hard substrates (Voultziadou et al. 2010, Navarro-Barranco et al. 2014, 2016). This complexity in the space-limited oligotrophic environment of the dark caves could be particularly significant for the motile cave dwellers. However, the motile invertebrate diversity of Mediterranean marine caves has received limited interest compared with the sessile biota; the few relevant studies have mainly taken place in the northwestern Mediterranean Sea (Ledoyer 1965, Navarro-Barranco et al. 2014, 2016), while such data are lacking from the eastern basin (but see Gerovasileiou et al. 2015b).

From the trophic point of view, marine caves are considered simple systems in which organic supply depends on the circulation of water entering the cave, given the absence of primary production due to lack of light (Bianchi et al. 2003). The trophic structure of Mediterranean caves is insufficiently studied, concerning only the feeding habits of polychaetes (Bianchi 1985) and amphipods (Navarro-Barranco et al. 2013). Equally understudied is the trophic structure of benthic invertebrate-associated assemblages, except for that of the anthozoans *Cladocora caespitosa* (Chintiroglou 1996) and *Astroides calycularis* (Terrón-Siglera et al. 2016). Taking into account the above, it would be interesting to investigate the role of sponges for the cave environment from a trophic point of view.

The aim of this study was (a) to contribute to the knowledge of motile macrobenthos in caves of the

eastern Mediterranean Sea and (b) to examine the hypothesis that different sponge species, previously found to host rich macrofaunal assemblages in shallow rocky beds of the same biogeographic area, maintain their role as ecosystem engineers or “living hotels” in the cave environment. To this end, we examined the taxonomic and trophic structure of the sponge-associated assemblages in two eastern Mediterranean marine caves.

MATERIALS AND METHODS

Study area

This study was conducted in two submerged caves of Lesvos Island, located in the North Aegean Sea: Fara cave (38°58'11.64"N, 26°28'39.54"E) and Agios Vasilios cave (38°58'13.25"N, 26°32'30.46"E). The caves are located at a different depth range (Fara: 11-18 m; Agios Vasilios: 24-40 m) and also belong to distinct morphological types: a submerged tunnel and a funnel-shaped blind cave respectively. Detailed morphological description and three-dimensional models of the caves are presented in Gerovasileiou et al. (2013) and Gerovasileiou and Voultziadou (2016). The sponge assemblages of these caves have been well-studied and are considered among the richest Mediterranean marine caves in terms of sponge diversity (Gerovasileiou and Voultziadou 2012).

Sampling and sample processing

The selection of sponges for the study of their associated fauna in the surveyed caves was based on the following criteria: (a) species with massive/tubular growth forms bearing conspicuous cavities and canals, (b) relatively abundant species with a broad distribution along the horizontal cave axis, and (c) species having been found to host a rich associated fauna in other habitat types in the Aegean Sea, for comparison purposes. The two species that fulfilled the above criteria in the two studied caves were *Agelas oroides* (Schmidt, 1864) and *Aplysina aerophoba* (Nardo, 1833). Previous studies in shallow rocky beds of the North Aegean Sea (3-10 m) had shown that these sponges host a species-rich associated fauna (Koukouras et al. 1985, Voultziadou-Koukoura et al. 1987, Koukouras et al. 1992). The role of these sponges as ecosystem engineers in marine caves is studied for the first time.

The species *A. oroides* was present in both caves (Fig. 1A-C), though it was quite rare in Agios Vasilios, with only few small-sized specimens developing mostly in the outer cave zone (Fig. 1E). On the other hand, *A. aerophoba* was abundant within the first 15 m of Agios Vasilios (Fig. 1D-E), but was absent from Fara cave and its surrounding area. Three specimens of the sponge *A. oroides* were collected from three distinct zones of Fara cave: the entrance (CE), the semidark zone (SD) and the inner dark zone (D) (Fig. 1A-C). The same sampling scheme was followed for the sponge *A. aerophoba* in Agios Vasilios cave, with the exception of the dark zone due to the local scarcity of this species

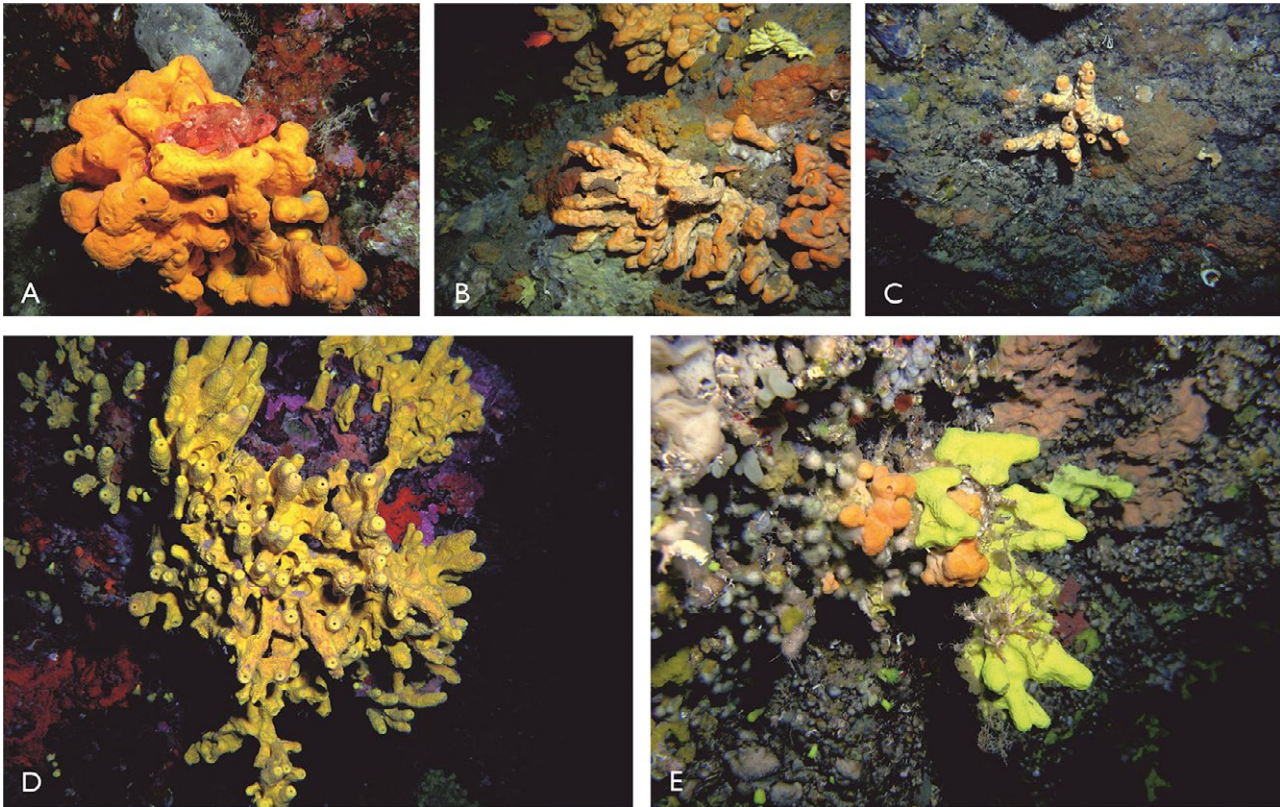


Fig. 1. – The sponge *Agelas oroides* at the entrance (A), semidark (B) and dark zone (C) of Fara cave and the sponge *Aplysina aerophoba* at the entrance (D) and semidark zone (E) of Agios Vasilios cave. A small-sized specimen of the sponge *Agelas oroides* has developed on the basis of the sponge *A. aerophoba* (E).

(few small-sized specimens). Replication was limited to the lowest possible level for extrapolating mean values of symbiont densities, in order to minimize the impact of sampling in confined cave zones where massive/tubular sponges had low abundance.

Sampling was performed using SCUBA in autumn 2009 (September–October). Sponge specimens were covered with 40×40 cm bags made of 0.5 mm mesh nylon nets to avoid loss of motile macrofauna (e.g. crustaceans) and were then detached using a knife. Samples were preserved in 10% formaldehyde.

Sponge volume was measured by water displacement. Sponges were then cut into small pieces along their canals and cavities and the associated fauna was removed. The water and the associated macrofauna, which remained in the bags, were washed through a 0.5-mm mesh sieve. Sponge-associated fauna was sorted, counted and identified to the lowest taxonomic level. Density of the identified taxa (abundance/sponge volume in cm³) was calculated, as the collected sponges varied in size.

Statistical and faunal analysis

Multivariate resemblance analysis of the associated fauna of the two sponges was performed with multidimensional scaling, based on the Bray-Curtis similarity index (square root transformed density data). The contribution of associated species to Bray-Curtis dissimilarity among the resulting sample groups was estimated with SIMPER (SIMilarity PERcentages).

One-way PERMANOVA was used in order to investigate the difference in the structure of the associated assemblage of (a) the examined sponge species (factor, Sponge species; fixed with two levels, *A. oroides* and *A. aerophoba*), and (b) specimens from different cave zones for each sponge species separately (factor, Zone; fixed with three levels for *A. oroides*, CE, SD and D; fixed with two levels for *A. aerophoba*, CE and SD), following the recommendations of Anderson et al. (2008). In cases of low numbers of unique permutations, P-values were obtained through a Monte Carlo test (Anderson et al. 2008).

Three diversity indices were calculated for the sponge-associated fauna, based on density of symbionts in every sponge specimen: number of taxa, Shannon-Wiener diversity (H'), and species evenness (J'). Variability of these indices across the distinct zones of the surveyed caves was investigated using one-way permutational ANOVA (perANOVA) under the same design that was used in above-mentioned PERMANOVA. Spearman's rank correlation coefficient was used to examine the relationship of sponge volume with the abundance and number of taxa of the associated fauna. The cumulative number of taxa was plotted against the cumulative volume for each sponge species to estimate the asymptotic number of taxa with increase in habitat space.

For the trophic characterization of the sponge-associated fauna, we studied the two faunal groups that showed the highest number of taxa and abundance: polychaetes and crustaceans. Polychaetes were as-

Table 1. – Macrofaunal symbionts found in the sponges *Agelas oroides* and *Aplysina aerophoba* in the studied caves (* first record as sponge symbionts; † first record as symbiont of *A. oroides*; ‡ first record as symbiont of *A. aerophoba*; FG, feeding group; c, carnivore; d, deposit-feeder or detritivore; f, filter-feeder; n, non-feeder; o, omnivore; CE, cave entrance; SD, semidark zone; D, dark zone).

Taxa of sponge-associated fauna	FG	<i>Agelas oroides</i>			<i>Aplysina aerophoba</i>	
		CE	SD	D	CE	SD
Nemertea				+	+	+
Nematoda				+	+	+
Polychaeta						
<i>Amphiglena mediterranea</i> (Leydig, 1851) †	f	+				
<i>Amphinome</i> sp.	c				+	
<i>Amphitrite</i> sp.	d	+				
<i>Boccardia polybranchia</i> (Haswell, 1885) * † ‡	d	+	+	+	+	+
<i>Branchiomma bombyx</i> (Dalyell, 1853)	f					+
<i>Ceratonereis (Composetia) costae</i> (Grube, 1840)	c				+	+
<i>Chone collaris</i> Langerhans, 1881 †	f			+		+
<i>Chrysopetalum debile</i> (Grube, 1855)	c				+	
<i>Dipolydora armata</i> (Langerhans, 1880) * †	d		+			
<i>Dodecaceria concharum</i> Örsted, 1843 ‡	d				+	
<i>Eupolyommia nebulosa</i> (Montagu, 1818) †	d	+				
<i>Eupolyommia nesidensis</i> (Delle Chiaje, 1828) †	d			+		
<i>Exogone (Exogone) naidina</i> Örsted, 1845 †	o	+				
<i>Exogone</i> sp.	o		+			
<i>Glycera tridactyla</i> Schmarda, 1861 * † ‡	c	+			+	
<i>Harmothoe spinifera</i> (Ehlers, 1864)	c	+			+	
<i>Leodice torquata</i> (Quatrefages, 1866)	c	+				
<i>Lumbrineris funchalensis</i> (Kinberg, 1865)	o				+	
<i>Lysidice ninetta</i> Audouin & Milne-Edwards, 1833	o	+		+		
<i>Myrianida</i> sp.	c				+	+
<i>Neanthes caudata</i> (Delle Chiaje, 1827) ‡	o				+	
<i>Nereis zonata</i> Malmgren, 1867	c		+	+	+	
<i>Notomastus latericeus</i> Sars, 1851 †	d	+				
<i>Oxydromus</i> sp.	c			+		
<i>Palola siciliensis</i> (Grube, 1840)	o		+			
<i>Perinereis</i> sp.	o	+			+	+
<i>Phyllodoce</i> sp.	c				+	
Phyllodocidae sp.	c		+			
<i>Placostegus tridentatus</i> (Fabricius, 1779) † ‡	f		+		+	
<i>Platynereis dumerilii</i> (Audouin & Milne-Edwards, 1834)	o		+			
Polychaeta sp.					+	
<i>Polydora hoplura</i> Claparède, 1869 †	d		+		+	
<i>Polyophthalmus pictus</i> (Dujardin, 1839) †	d	+				
<i>Pontogenia chrysocoma</i> (Baird, 1865) ‡	c					+
<i>Potamilla torelli</i> (Malmgren, 1866)	f	+				
<i>Prionospio malmgreni</i> Claparède, 1869 * †	d	+				
<i>Pseudopotamilla reniformis</i> (Bruguère, 1789)	f	+	+	+	+	
<i>Salvatoria</i> sp.	c					+
<i>Sphaerosyllis bulbosa</i> Southern, 1914 * ‡	d					+
<i>Sphaerosyllis hystrix</i> Claparède, 1863 † ‡	d		+		+	+
<i>Spio filicornis</i> (Müller, 1776) †	d	+	+			
<i>Spiophanes</i> sp.	d				+	
<i>Spirobranchus polytrema</i> (Philippi, 1844)	f	+			+	+
<i>Spirorbis</i> sp.	f	+				+
<i>Subadyte pellucida</i> (Ehlers, 1864)	c				+	+
<i>Syllidia armata</i> Quatrefages, 1866 †	c	+				
<i>Syllis amica</i> Quatrefages, 1866	c	+	+	+		+
<i>Syllis armillaris</i> (O.F. Müller, 1776)	o	+				
<i>Syllis gracilis</i> Grube, 1840	o				+	
<i>Syllis hyalina</i> Grube, 1863	o	+			+	+
<i>Syllis variegata</i> Grube, 1860	o	+		+		
<i>Vermiliopsis infundibulum</i> (Philippi, 1844)	f		+			
<i>Vermiliopsis labiata</i> (O. G. Costa, 1861) * ‡	f					+
<i>Vermiliopsis monodiscus</i> Zibrowius, 1968 * † ‡	f	+				+
Sipuncula						
<i>Aspidosiphon (Aspidosiphon) muelleri muelleri</i> Diesing, 1851		+	+		+	+
<i>Phascolosoma (Phascolosoma) granulatum</i> Leuckart, 1828			+			
Crustacea						
Copepoda						
Copepoda sp. 1					+	+
Copepoda sp. 2					+	
Decapoda						
Anomura sp.	o					+
<i>Athanas nitescens</i> (Leach, 1813 [in Leach, 1813-1814])	o	+			+	
<i>Eualus occultus</i> (Lebour, 1936)	o	+			+	+
Tanaidacea						
<i>Leptocheilia savignyi</i> (Krøyer, 1842)	d			+	+	+
<i>Paradoxapseudes intermedius</i> (Hansen, 1895) * † ‡	d	+		+	+	+
Isopoda						
<i>Gnathia vorax</i> (Lucas, 1849)	n	+	+	+		
<i>Janira maculosa</i> Leach, 1814	d	+	+	+	+	+

Taxa of sponge-associated fauna	FG	<i>Agelas oroides</i>		D	<i>Aplysina aerophoba</i>	
		CE	SD		CE	SD
Amphipoda						
<i>Colomastix pusilla</i> Grube, 1861	c	+	+	+	+	+
<i>Leptocheirus bispinosus</i> Norman, 1908 * † ‡	d	+		+	+	+
<i>Leucothoe spinicarpa</i> (Abildgaard, 1789)	c	+			+	+
<i>Liljeborgia dellavallei</i> Stebbing, 1906 ‡	c				+	+
<i>Phthisica marina</i> Slabber, 1769 ‡	o				+	+
<i>Stenothoe</i> sp.	o					+
Cumacea						
Cumacea sp.					+	
Mollusca						
Gastropoda						
<i>Bittium reticulatum</i> (da Costa, 1778)			+			
<i>Vitreolina incurva</i> (Bucquoy, Dautzenberg & Dollfus, 1883) * †		+				
Vermetidae sp.					+	
<i>Raphitoma</i> sp.		+				
<i>Tyrodina perversa</i> (Gmelin, 1791)					+	+
Bivalvia						
<i>Hiatella arctica</i> (Linnaeus, 1767)		+	+		+	+
<i>Lithophaga lithophaga</i> (Linnaeus, 1758) ‡						+
<i>Modiolus barbatus</i> (Linnaeus, 1758) ‡					+	
Echinodermata						
Ophiurida						
<i>Amphipholis squamata</i> (Delle Chiaje, 1828) †						+
<i>Ophiothrix fragilis</i> (Abildgaard, in O.F. Müller, 1789)					+	
Chordata						
Perciformes						
<i>Lepadogaster candolii</i> Risso, 1810 * ‡						+
<i>Corcyrogobius liechtensteini</i> (Kolombatovic, 1891) * †		+				
Total number of taxa		37	21	18	44	36

Table 2. – Taxa of symbionts per taxonomic group for the sponges *Agelas oroides* and *Aplysina aerophoba* in the studied caves (CE, entrance; SD, semidark zone; D, dark zone).

	Both sponges		<i>Agelas oroides</i>		CE	SD	D	<i>Aplysina aerophoba</i>			
	Total	Common	Exclusive	Total				Exclusive	Total	CE	SD
Nemertea	1	1		1			1		1	1	1
Nematoda	1	1		1			1		1	1	1
Polychaeta	54	15	22	37	24	14	9	17	32	23	17
Sipuncula	2	1	1	2	1	2			1	1	1
Crustacea	16	8	1	9	8	3	6	7	15	13	12
Amphipoda	6	3		3	3	1	2	3	6	5	6
Copepoda	2								2	2	1
Cumacea	1								1	1	
Decapoda	3	2		2	2			1	3	2	2
Isopoda	2	1	1	2	2	2	2		1	1	1
Tanaidacea	2	2		2	1		2		2	2	2
Mollusca	8	1	3	4	3	2		4	5	4	3
Gastropoda	5		3	3	2	1		2	2	2	1
Bivalvia	3	1		1	1	1		2	3	2	2
Echinodermata	2		1	1			1	1	1	1	
Pisces	2		1	1	1			1	1		1
Total	86	27	29	56	37	21	18	30	57	44	36

signed to feeding groups based on data from Fauchald and Joumars (1979), Chintiroglou (1996), Antoniadou and Chintiroglou (2005), Antoniadou (2014), Faulwetter et al. (2014) and the World Register of Marine Species (WoRMS) (www.marinespecies.org). Crustaceans were also assigned to feeding groups according to data from Hazlet (1962), Gambi et al. (1992), Birkely and Gulliksen (2003), Tanaka (2007), Voultsiadou et al. (2007), Navarro-Barranco et al. (2013), Guerra-Garcia et al. (2014) and WoRMS. Number of taxa and abundance per feeding group were measured for the two studied sponges, while density of symbionts per feeding group was calculated for every sponge specimen. Variability of density per feeding group was examined using perANOVA under the aforementioned design.

Statistical analyses were performed with the IBM SPSS Statistics 21 and the PRIMER 6 and PERMANOVA+ software packages (Clarke and Gorley 2006).

RESULTS

A total of 3037 macrofaunal specimens were collected from the canals and cavities of the 15 examined sponges. The identification of sponge symbionts yielded 86 taxa belonging to 8 major groups (Table 1). The sponge *A. aerophoba* (Agios Vasilios cave) showed higher abundance of macrofaunal symbionts (2587 specimens) than *A. oroides* (Fara cave) (450 specimens). However, almost equal numbers of taxa were found in both sponge species (57 taxa in *A. aerophoba* and 56 taxa in *A. oroides*), with 27 taxa being present in both sponges (Table 2). Crustaceans, mainly Amphipoda and Isopoda, dominated in terms of abundance in both sponges (91% of symbionts in *A. aerophoba* and 65% in *A. oroides*), while polychaetes prevailed regarding the number of taxa (51% and 65% of symbiotic taxa respectively) (Fig. 2).

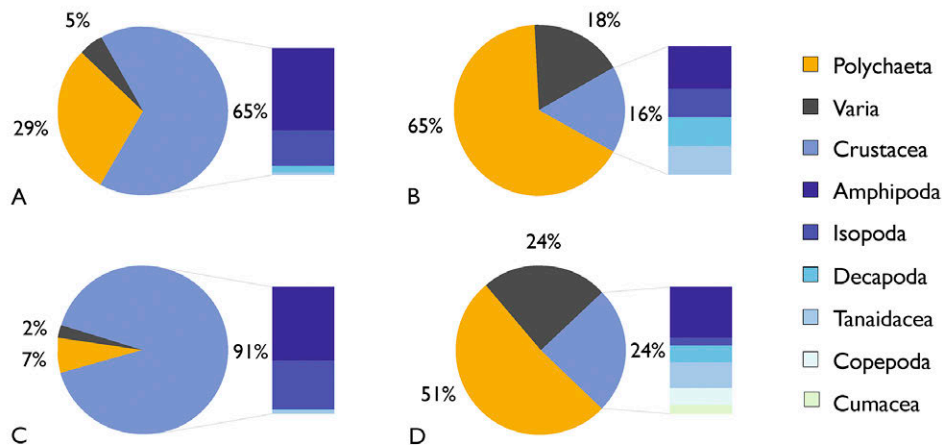


Fig. 2. – Taxonomic composition of the associated fauna of the sponges *Agelas oroides* (A: abundance, B: number of taxa) and *Aplysina aerophoba* (C: abundance, D: number of taxa). The group “Varia” includes Nemertea, Nematoda, Sipuncula, Mollusca, Echinodermata and Pisces.

Table 3. – Spearman’s rank correlation coefficient (ρ) between the sponge volume and the abundance (N) and species number (S) of symbionts (**significance at the 0.01 level; *significance at the 0.05 level).

	<i>Agelas oroides</i>		<i>Aplysina aerophoba</i>		Both species	
	N	S	N	S	N	S
ρ	0.899	0.252	0.714	0.377	0.809	0.599
P-value	0.001**	0.513	0.111	0.461	0.000**	0.018*
N	9	9	6	6	15	15

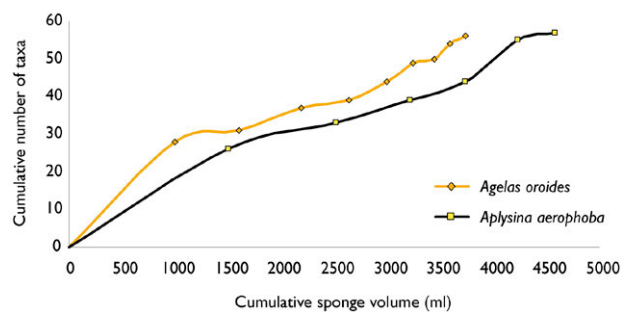


Fig. 3. – Cumulative curves of number of taxa per sponge volume for *Agelas oroides* and *Aplysina aerophoba*.

A positive correlation was found between the sponge volume and the number of symbiotic taxa for both sponges (Table 3), but it was significant only for *A. oroides*. A significant positive correlation was found between the sponge volume on the one hand, and the abundance and number of symbiotic taxa on the other, when all 15 specimens of the two sponge species were examined together. The cumulative number of symbiotic taxa did not approach an asymptotic value when plotted against cumulative sponge volume, for either of the two sponges (Fig. 3).

Resemblance analysis showed clear differentiation in the assemblage structure of the associated fauna between the two sponge species, with a dissimilarity of 75% (Fig. 4). Specimens of *A. aerophoba* from different zones of Agios Vasilios cave showed similarity higher than 56% among each other, while those of *A. oroides* from Fara cave showed a similarity of only 35.5%. Results of one-way PERMANOVA revealed significant difference in the composition of the asso-

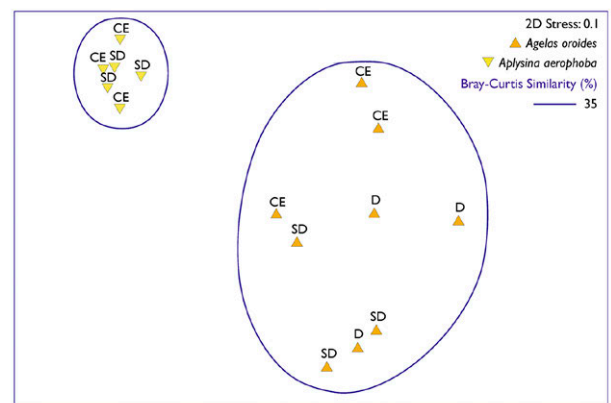


Fig. 4. – Resemblance of sponge-associated assemblages of the sponge species *Agelas oroides* and *Aplysina aerophoba*, collected from distinct cave zones (CE: entrance, SD: semidark zone, D: dark zone).

ciated assemblages of the two sponge species (Table 4). When each sponge was examined separately, no significant differences were found in their associated assemblage structure in the different cave zones. SIMPER analysis between the associated fauna of the two sponge species showed that nine macrobenthic species (i.e. *Janira maculosa*, *Colomastix pusilla*, *Gnathia vorax*, *Leptochelia savignyi*, *Boccardia polybranchia*, *Eualus occultus*, *Liljeborgia dellavallei*, *Leucothoe spinicarpa* and *Pseudopotamilla reniformis*) contributed 55% to the Bray-Curtis dissimilarity index.

The specimens of *A. aerophoba* examined across Agios Vasilios cave showed higher density and number of symbiotic taxa than those of *A. oroides* across Fara cave; the opposite trend was found for species diversity (H') and evenness (J') (Fig. 5). The total number of sym-

Table 4. – Summary of results of one-way PERMANOVA for the associated fauna of the two sponge species. Analyses were performed on square root-transformed density data, based on Bray-Curtis similarity index (**significance at the 0.01 level).

Source of variability	d.f.	SS	MS	F	P
Sponge species	1	12076	12076	8.3004	0.001**
Residual	13	18914	1454.9		
Total	14	30990			

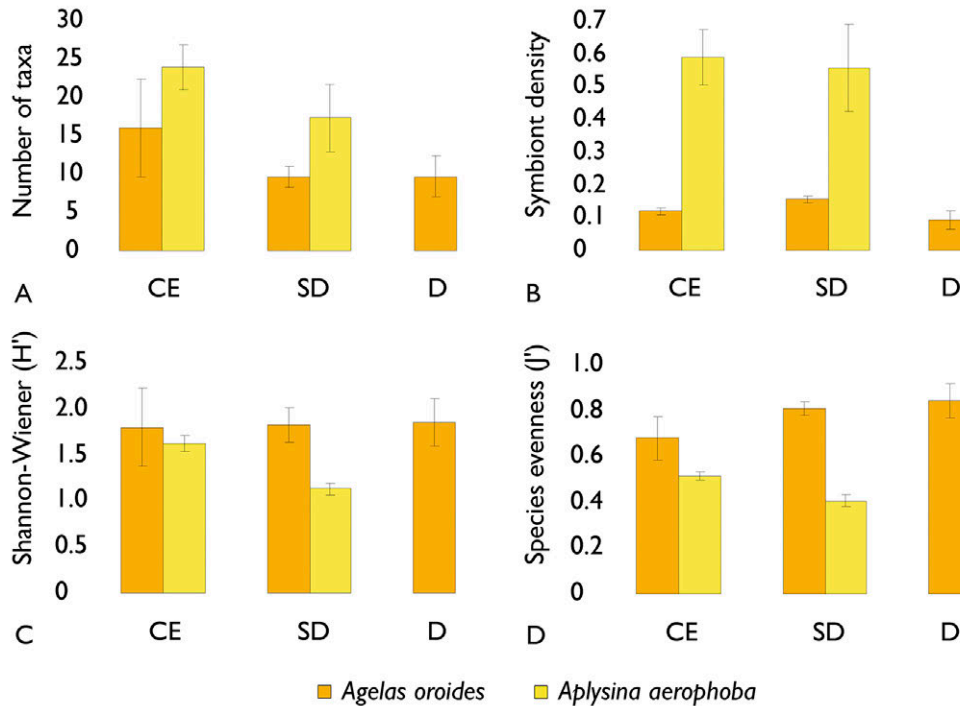


Fig. 5. – Mean number of taxa (A), density (B), Shannon-Wiener diversity (C) and species evenness (D) of symbionts for the sponges *Agelas oroides* and *Aplysina aerophoba* across the surveyed caves (CE, entrance; SD, semidark zone; D, dark zone). Standard error of mean is presented in error bars.

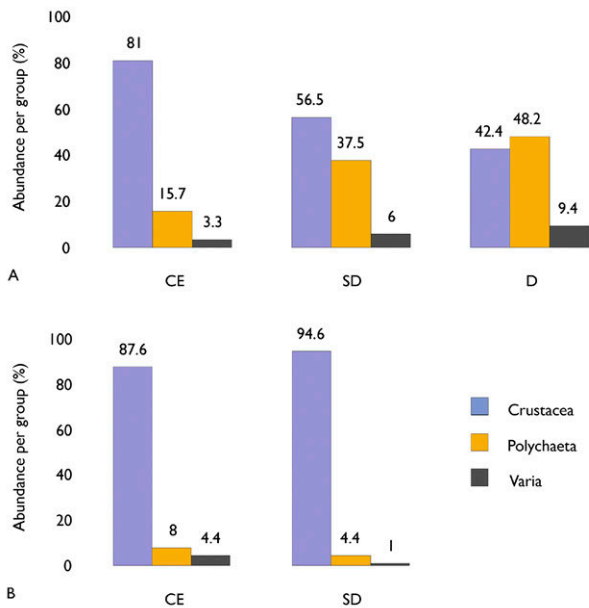


Fig. 6. – Abundance of symbionts per taxonomic group found in the examined specimens of *Agelas oroides* (A) and *Aplysina aerophoba* (B) across the surveyed caves (CE, entrance; SD, semidark zone; D, dark zone).

biotic taxa decreased from the entrance to the interior of the two caves for both sponge species (Table 2); samples of *A. oroides* from the dark interior of Fara cave showed half the number of associated taxa (18) compared with those from the entrance (37). The mean abundance of polychaetes associated with the sponge *A. oroides* increased towards the dark zone of Fara cave, with a parallel decrease of crustaceans (Fig. 6). The mean number of associated taxa decreased (Fig. 5A) towards the cave

interior for both species, while the mean density of symbionts remained stable (Fig. 5B). Values of species diversity (Fig. 5C) and evenness (Fig. 5D) increased towards the cave interior for the species *A. oroides*, while the opposite trend was found for *A. aerophoba*. However, results of perANOVA showed that none of the above changes were statistically significant.

The trophic characterization of the sponge-associated polychaetes and crustaceans revealed five feeding groups: carnivores (19 taxa), deposit-feeders or detritivores (18), omnivores (17), filter-feeders (11) and one non-feeder (see Table 1). Deposit-feeders (mainly polychaetes) were the species-richest feeding group (33%) in the sponge *A. oroides*, while carnivores (basically crustaceans) were the most abundant (48%) (Fig. 7). On the other hand, in *A. aerophoba* carnivores dominated in terms of both number of taxa (35%) and abundance (55%). The isopod *G. vorax*, which in the adult, sponge-associated, stage is non-feeding, was found only in *A. oroides*.

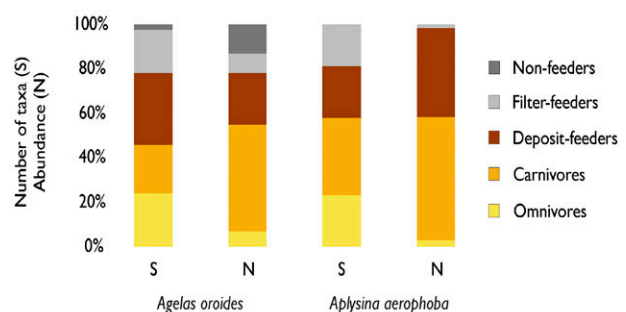


Fig. 7. – Trophic structure of sponge-associated polychaetes and crustaceans in terms of number of taxa (S) and abundance (N).

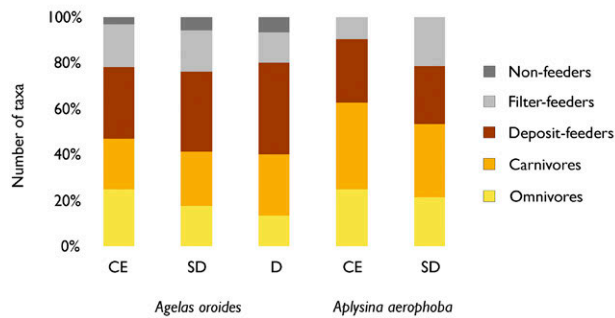


Fig. 8. – Trophic structure, in terms of number of taxa, of sponge-associated polychaetes and crustaceans across the surveyed caves (CE, entrance; SD, semidark zone; D, dark zone).

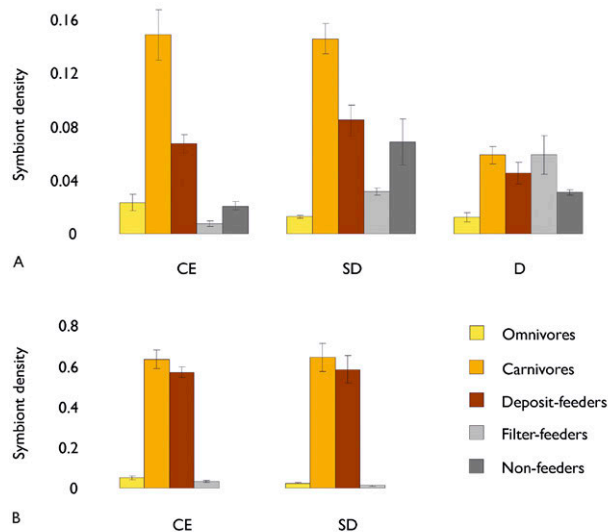


Fig. 9. – Mean density of symbionts (polychaetes and crustaceans) per feeding group for the sponges *Agelas oroides* (A) and *Aplysina aerophoba* (B) across the surveyed caves (CE, entrance; SD, semidark zone; D, dark zone). Standard error of mean is presented in error bars.

The trophic composition, in terms of number of taxa, of the sponge-associated polychaetes and crustaceans did not change significantly across the distinct cave zones for both sponge species (Fig. 8). The mean density of carnivores decreased towards the dark cave zone in the sponge *A. oroides*, while that of filter-feeders and non-feeders increased (Fig. 9). However, none of these changes was statistically significant, with the exception of the non-feeding isopod *G. vorax*, which showed the highest density in the semidark zone (Pseudo-F=2.5543, $p < 0.05$, $df=8$). No changes were found for the symbiont density of any feeding group in the sponge *A. aerophoba*.

DISCUSSION

Although sponges dominate in marine caves, their role as ecosystem engineers is being studied here for the first time. Our results revealed that the sponge species *A. aerophoba* and *A. oroides* in the two studied caves supported a considerable associated macrofauna. Twelve macrofaunal species found in this study are reported for the first time as sponge symbionts, 22 as symbionts of *A. oroides*, and 17 as symbionts of *A.*

aerophoba (Table 1). Most of these species (around 70%) have been previously recorded in Mediterranean marine caves (Gerovasileiou et al. 2015b). Characteristic examples include the polychaete *Vermiliopsis monodiscus*, which is considered a typical species of cave communities in the northwestern Mediterranean (Zibrowius 1968), and the Liechtenstein's goby, *Coryrogobius liechtensteini*, which finds shelter in shadowy micro-habitats within caves (Gerovasileiou et al. 2015a). Both species are reported here for the first time as sponge symbionts.

The dominance of crustaceans (mostly amphipods and isopods), followed by polychaetes, in terms of abundance in both sponge species, is in accordance with previous studies (Pansini 1970, Koukouras et al. 1992, 1996, Ribeiro et al. 2003). The numeric dominance of amphipods in sponges could be related to their small size providing ease in movement along the sponge canals (Koukouras et al. 1985, Voultsiadou-Koukoura et al. 1987). Koukouras et al. (1985) found that crustaceans (mainly amphipods) dominated in *A. aerophoba*, but that the infaunal assemblage of *A. oroides* was equally represented by crustaceans and polychaetes.

Mean density of symbionts of *A. aerophoba* was 5-6 times higher than that of *A. oroides*, as previously found for other habitat types in the same biogeographic area (Koukouras et al. 1992, 1996). Koukouras et al. (1996) estimated that *A. aerophoba* has higher complexity (in terms of canal volume and mean canal diameter) than *A. oroides*, to which they attributed the higher abundance and species number of its symbiotic assemblage. In our case, despite the fact that density and number of taxa showed higher values in *A. aerophoba*, Shannon-Wiener and species evenness indices had higher values in *A. oroides*, as found by Koukouras et al. (1992). This is probably related to the dominance of two peracarids, *Colomastix pusilla* and *Janira maculosa*, in *A. aerophoba*. The convergence of our results regarding quantitative taxonomic composition of the sponge-associated fauna with those of studies conducted four decades ago at different sites, depths and habitat types of the same geographic area, the North Aegean Sea (Koukouras et al. 1985, Voultsiadou-Koukoura et al. 1987, Koukouras et al. 1992, 1996), verifies that sponges support well-structured macrofaunal assemblages, consisting of species with particular ecological habits.

A notable portion of the macrofauna found in this study (organisms identified to the species level) has been recorded before in the sponges *A. oroides* and *A. aerophoba* (45% and 67% of the species, respectively). Typical sponge-endobionts include the isopod *J. maculosa*, the amphipods *C. pusilla* and *Leucothoe spinicarpa* and the bivalve *Hiatella arctica*; the ophiurid *Ophiothrix fragilis* has also been commonly reported as a sponge-epibiont (Koukouras et al. 1985). The high abundance of some of these species has been attributed either to parasitism (e.g. the amphipod *L. spinicarpa* according to Connes 1967) or to specific stages of their life cycle, such as recruitment (Turon et al. 2000). Sponges have been reported to function as “reproduc-

tive centres” or “resting places” for larvae and adults of several macrobenthic species (Klitgaard 1991, Turon et al. 2000). This was also evidenced in our study but only for sponge specimens collected near the cave entrance; juveniles of the amphipod *C. pusilla* and egg-carrying individuals of the tanaid *Paradoxapseudes intermedius* were found in the cavities of *A. oroides*, while egg-carrying individuals of the decapods *Athanas nitescens* and *Eualus occultus* were found in the sponge *A. aerophoba*.

The analysis of the trophic structure of the sponge-associated polychaete and crustacean assemblages showed an almost even distribution of taxa among feeding types. The slight prevalence of deposit-feeders in *A. oroides* and carnivores in *A. aerophoba* highlights the differences between the two sponge species, as discussed above. Concerning abundance, the dominance of carnivores in both sponges, which is mainly attributed to the amphipod *C. pusilla*, is in accordance with the findings of Navarro-Barranco et al. (2013) on amphipod assemblages in cave sediments. The absence of herbivores is attributed to the lack of primary producers in the cave environment (Harmelin et al. 1985). Non-feeders were represented only by the isopod *G. vorax*, which has a biphasic life cycle, with the adults inhabiting cryptic environments like sponges (Tanaka 2007). Although the trophic structure of the entire sponge-associated assemblage did not change between cave zones, non-feeders showed an increase in density inwards; this might be due to the fact that they are not affected by the decrease in trophic input towards the cave interior but only by the availability of suitable habitat (i.e. the sponge-dominated semidark cave zone). The feeding preferences of a given species may vary with environment, as shown by Terrón-Siglera et al. (2016), who found that typical carnivorous amphipods mainly fed on detritus inside the colonies of the coral *Astroides calycularis*. On the other hand, Navarro-Barranco et al. (2013) found no significant differences between caves and nearby open habitats in the gut content of sediment amphipods. A thorough study of the feeding habits of typical sponge associates could enhance understanding of the trophic web in sponge-dominated habitats such as marine caves.

The results of multivariate analyses in this study highlighted differences in the structure of macrofaunal assemblages of the examined sponges. This high dissimilarity was mainly attributed to several species, which could be divided into the following categories: (a) species with higher abundance in *A. aerophoba* (e.g. the crustaceans *J. maculosa*, *C. pusilla*, *Leptocheilia savignyi* and *E. occultus*); (b) species with higher abundance in the sponge *A. oroides* (e.g. the polychaetes *Boccardia polybranchia* and *Pseudopotamilla reniformis*); (c) species found only in *A. oroides* (e.g. the isopod *G. vorax*); and (d) species found only in *A. aerophoba* (e.g. the amphipods *Liljeborgia dellavallei* and *Leucothoe spinicarpa*). Previous studies on the associated fauna of these two sponges in sublittoral rocky reefs showed that the Bray-Curtis similarity index between the two sponges was over 50%, as half of the symbionts were commonly found in both sponges

(Koukouras et al. 1992, 1996). In this study, the number of common symbionts was slightly lower (47-48%).

The considerable number of newly recorded macrofaunal species in the examined sponges (30% of *A. aerophoba* and 39% of *A. oroides* symbionts) indicates the potential influence of the marine cave environment on the associated assemblage structure. Interestingly for both sponges, the majority (59%) of the newly recorded symbionts were found exclusively in one cave. Thus, dissimilarity between the associated assemblages of the two sponges could be partially attributed to the fact that they were collected in different caves with different geomorphological and ecological characteristics (Gerovasileiou et al. 2013, Gerovasileiou and Voultsiadou 2016). Marine caves are commonly acknowledged for their “idiosyncratic behaviour” regarding the prevailing environmental features and their sessile and motile fauna (Martí et al. 2004, Bussotti et al. 2006, Navarro-Barranco et al. 2013). The influence of the surrounding environment on the composition of sponge-associated assemblages has been observed for temperate sublittoral rocky beds and *Posidonia* meadows (Koukouras et al. 1996, Gherardi et al. 2001). In support of this, none of the macrofaunal species found associated with the sponges *A. aerophoba* and *A. oroides* in the two caves can be considered an obligate sponge symbiont: they are either sciaphilic species finding shelter in cryptic micro-habitats, including caves, or euryoecious species dwelling in a wide range of marine habitats (Ledoyer 1965, Koukouras et al. 1985, 1996).

The fact that the cumulative number of symbiotic species did not approach an asymptotic value when plotted against cumulative sponge volume for either of the two sponges possibly shows that further sponge sampling in the studied caves would increase the number of associated species. The positive relationship of sponge volume with number of taxa and abundance of associated fauna has been previously shown for *A. aerophoba* and *A. oroides* (Koukouras et al. 1992), as well as for other sponge species (Gherardi et al. 2001, Çınar et al. 2002).

The decrease in the total number of sponge-associated taxa towards the inner dark zone of Fara cave seems to follow the general diversity patterns described for several Mediterranean caves (Balduzzi et al. 1989, Martí et al. 2004, Gerovasileiou and Voultsiadou 2016). This is most likely due to the fact that environmental features, such as algal coverage and hydrodynamic regime, seem to affect diversity of sponge-associated fauna, as has been shown for open environments (Voultsiadou-Koukoura et al. 1987, Çınar et al. 2002). In accordance with this finding, Navarro-Barranco et al. (2014) suggested that the absence of macroalgae along with the increasing oligotrophy were responsible for a significant reduction in the diversity of motile epifauna from the open rocky substrates close to the cave mouth towards the inner semidark cave sectors. However, in our case, the mean density and diversity, as expressed by the examined indices, did not vary significantly along the horizontal axis of the surveyed caves, implying that sponges provide quite

stable micro-habitat for the associated organisms. This is further supported by the observation that the qualitative and quantitative trophic structure of the sponge-associated fauna did not significantly change between cave zones. These findings become particularly important in the inner impoverished parts of the caves, where micro-habitats are generally lacking due to the low biotic coverage and the local dominance of few sessile invertebrates with encrusting growth forms (Gerovasileiou and Voultziadou 2016 and references therein). The presence of habitat-forming organisms, such as the massive/tubular sponges, becomes critical for motile diversity by adding three-dimensional complexity to the assemblages and providing a habitat for a variety of species, as Navarro-Barranco et al. (2016) have shown for crustaceans in semidark caves. The scarcity or even absence of benthic invertebrates with a massive or dendritic form, other than Porifera, in eastern Mediterranean marine caves (Gerovasileiou et al. 2015b) could be indicative of their significance for these habitats. Furthermore, this might have interesting implications for the energy-transfer by motile fauna, as shown for mysids (Coma et al. 1997), in dark cave zones, which have been characterized as “extreme” oligotrophic environments (Harmelin et al. 1985).

In conclusion, the results of this study support the initial hypothesis that sponges maintain their functional role as ecosystem engineers across the studied marine caves, as shown by the study of both the taxonomic and trophic structure of their associated assemblages. However, in order to better understand the engineering function of sponges in marine caves, further study is required in different caves and areas, including comparisons of their associated macrofauna with the cave-dwelling motile macrofaunal assemblages. Such research, besides shedding light on the role of sponges, might also reveal interesting findings about the functioning of the peculiar cave environment itself.

ACKNOWLEDGEMENTS

We thank Maria Sini and Drosos Koutsoubas for their help during fieldwork, Asimena Gavriilidou for her help during laboratory work, Charalampos Dimitriadis for assistance in statistical analysis and Carlos Navarro-Barranco for providing the Spanish summary text and helping with the assignment of crustaceans to feeding groups. This research was co-financed by the EU Social Fund and Greek national funds through the “Heracleitus II” Research Funding Programme. The first author also benefited from an “Alexander S. Onassis Public Benefit Foundation” fellowship.

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