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Shallow-water sponge grounds along the Apulian coast (central Mediterranean Sea)

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Abstract
Sponge grounds are complex three-dimensional benthic habitats dominated by sponges. These sponge-dominated assemblages have been reported worldwide, from the intertidal zone to the deep sea. In shallow euphotic waters, dense sponge aggregations have been mainly found in tropical areas, and their presence is in some cases related to environmental degradation and coral decline. The Mediterranean Sea is globally recognised as a biodiversity hotspot, where light-exposed rocky reefs are typically dominated by photophilous algae. However, high local anthropogenic pressures, coupled with climate change, are leading to the reorganisation of benthic communities and the occurrence of regime shifts in several areas. Here we report the first description of unusual, shallow-water sponge grounds in Mediterranean light-exposed rocky reefs, in an area previously impacted by the destructive date-mussel fishery. These assemblages, found along the Apulian coast (central Mediterranean Sea), are now (2017) characterised by a mean coverage of sponges ranging between 3% and 33%, with maximum values up to 85%. Variation in the structure of assemblages and in the abundance of individual taxa between depths has been tested by multivariate and univariate techniques. The spatial characterisation has been complemented with the taxonomic analysis of the sponge assemblages, which resulted in the identification of 14 sponge taxa. These findings are compared with results of previous research in the same area and discussed with particular reference to the potential variables involved in sponge dominance and spatial distribution in the present system and elsewhere.

Keywords Porifera · Spatial distribution · Rocky subtidal · Barren habitat · Sponge-dominated habitat

Introduction

Sponges diverged from other metazoans over 600 million years ago and are now common sessile organisms in tropical, temperate, and polar benthic ecosystems (Brien et al. 1973; Srivastava et al. 2010; Bell et al. 2015). Sponges are considered important members of benthic marine ecosystems, as a result of their extensive distribution, large biomass in many habitats, and the number of ecological roles that they play (Bell 2008; Heip et al. 2009).

Sponge aggregations may create complex three-dimensional habitats, which, when characterised by large sponge biomass and space occupancy, are described as 'sponge grounds' (Heyward et al. 2010; Hogg et al. 2010; Bo et al. 2012; Murillo et al. 2012; Beazley et al., 2013; Maldonado et al. 2017). Sponge grounds are found in a variety of habitats, from the intertidal to the deep-sea environment (Maldonado et al. 2017).

In shallow waters, dense sponge aggregations have been reported in polar, temperate, and tropical ecosystems, and

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Francesca Strano and Valerio Micaroni are first co-authors.

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mainly in shaded or dark habitats such as caves, mesophotic reefs, and understoreys (Dayton et al. 1974; Bell and Barnes 2000; Corriero et al. 2000; Aronson et al. 2002; Bell 2002; Heyward et al. 2010; Gerovasileiou and Voultsiadou 2012).

However, in shallow light-exposed reefs, sponge-dominated communities have been only described in tropical regions, including Indo-Pacific, Central Pacific, Caribbean, and Brazilian coasts (Maldonado et al. 2017). In these areas, sponges may have become dominant on shallow rocky substrates because of environmental degradation responsible for mass mortality of corals (Aronson et al. 2002; Kelmo et al. 2013; Farnham and Bell 2018). Furthermore, there is evidence that, as a result of extreme thermal events, some sponge species can proliferate extensively, becoming dominant in the marine environment (Aronson et al. 2002; Kelmo et al. 2013). In Brazilian and Belizean reefs, for example, the El Niño-Southern Oscillation event in 1998 had devastating effects on hermatypic corals, while sponge abundance increased (Aronson et al. 2002; Kelmo et al. 2013), probably due to the higher tolerance of sponges to rapid temperature variations compared with other sessile taxa (Bell et al. 2013). Similarly, in both the Indonesian Wakatobi Marine National Park and the Palmyra Atoll in the Central Pacific reef, degradation led to a drastic reduction of corals as the dominant organisms, and their replacement by sponges (Bell and Smith 2004; Knapp et al. 2013).

More recently, the wider accessibility of ROV technology has led to the discovery of sponge-dominated habitats in the deep seas of all the oceans (Krautter et al. 2001; Klitgaard and Tendal 2004; Bo et al. 2012; Göcke and Janussen 2013; Bertolino et al. 2015; Howell et al. 2016; Mcintyre et al. 2016). These habitats are now recognised as reservoirs of biodiversity by the United Nations Environment Programme (UNEP) (Hogg et al. 2010). The development of such sponge aggregations is typically shaped by geological, hydrological, and biological gradients, and they may be important to the nutrient circulation in abyssal environments (Hogg et al. 2010; Kutti et al. 2013; Cathalot et al. 2015; Goodwin et al. 2017; Maldonado et al. 2017).

The Mediterranean Sea is a temperate basin with a rich biota that includes cold-temperate and subtropical species (Bianchi et al. 2012). Despite the small size, it has a very high number of species and degree of endemism, and is globally recognised as a hotspot of biodiversity (Coll et al. 2010). Mediterranean light-exposed rocky reefs of the open coast are typically dominated by photophilous algae, while shaded or dark reefs can be dominated by sciaphilous algae or invertebrates (Pérès and Picard 1964; Ballesteros 2006; Danovaro 2013). However, due to severe demographic, urban, and industrial pressures, combined with global climate change, Mediterranean biodiversity has been changing at an unprecedented rate in recent years, with the occurrence of several shifts in its biological settings (Bianchi and Morri 2000; Cuttelod et al. 2009; Lejeusne et al., 2010; Claudet and Fraschetti 2010; Coll et al. 2010; Bianchi et al. 2014).

In the last decades of the past century, some areas of the Mediterranean Sea, including the Apulian coasts, have been greatly affected by the date-mussel *Lithophaga lithophaga* fishery (Fanelli et al. 1994). This heavily destructive practice involves the demolition of the rocky substrate using SCUBA, sledgehammers and underwater vehicles to collect the living molluscs (Guidetti et al. 2003). It was documented that, after the destruction of the rock and the consequent elimination of all the sessile organisms, the substrata have been quickly colonised by the sea urchins *Arbacia lixula* and *Paracentrotus lividus*. Sea urchins, through unselective grazing, prevented the recolonisation by perennial macroalgae (Russo and Cicogna 1991; Bonaviri et al. 2011; Guidetti 2011).

Here we report the first quantitative and taxonomic characterisation of an unusual shallow-water (3–7 m of depth) sponge ground from a light-exposed rocky reef of the Mediterranean Sea. Possible biotic and abiotic factors triggering sponge dominance in this area are discussed.

Materials and methods

The study area

This study was carried out in August 2017, by SCUBA diving, along the south-western coast of the Salento Peninsula (Fig. 1). Sampling was performed in the framework of the project Biodiversity MARE Tricase (Micaroni et al. 2018a, 2018b). The estimated area characterised by the presence of extensive sponge assemblages corresponds to ~26 km^2. Sampling was conducted at the two sites where the shallow-water sponge grounds were present according to previous observations: site 1 (~1 km long), located at Santa Caterina, Nardò, Lecce, and site 2 (~6 km long), located at Porto Cesareo, Lecce. The two sites are ~13 km apart (Fig. 1), and site 2 is within the marine protected area of Porto Cesareo.

The coastline at the study area shows an alternation of sandy beaches and rocky shores, while the sampled shallow subtidal rocky habitat is characterised by well-illuminated and moderately exposed calcareous plateaus. Detailed information on the hydrological regime of the study area can be found in Parenzan (1983) and Rivaro et al. (2004). The benthic assemblages are typical of Mediterranean barrens, with a few erect macroalgae, including articulated corallines *Amphiroa* sp., sheet-like brown algae of the genus *Dictyota*, and the 'peacock's tail' brown alga *Padina pavonica* (Linnaeus) Thivy, 1960; main invertebrates include the sea urchins *Paracentrotus lividus* (Lamarck, 1816) and *Arbacia lixula* (Linnaeus, 1758), the endolithic bivalve *Lithophaga lithophaga* (Linnaeus, 1758), encrusting bryozoans, and

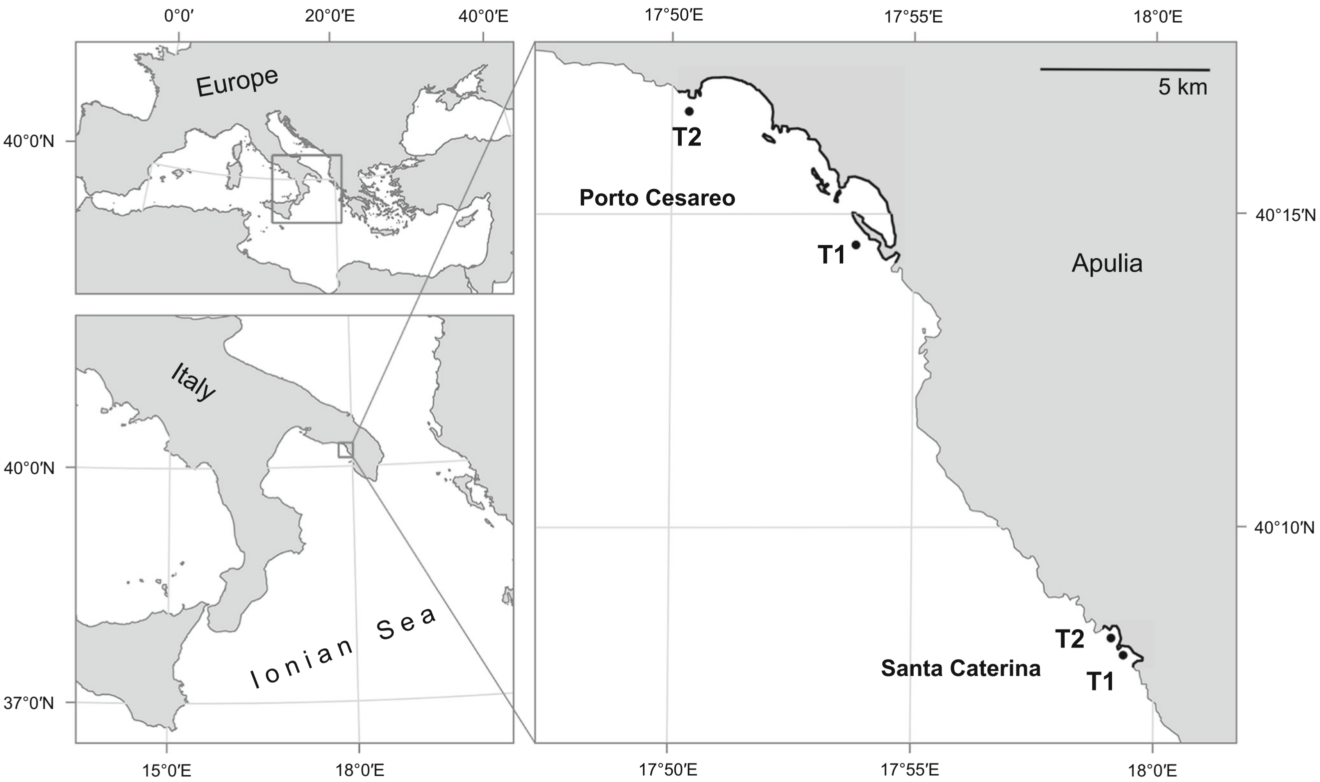

Fig. 1 Map of the study area. The maps on the right side show the position of the study area in the Mediterranean Sea and in in the south-east of the Italian peninsula. The map on the left side shows the location of the two sites: site 1 Santa Caterina, site 2 Porto Cesareo. T1 Transect 1, T2 Transect 2

sponges (Guidetti et al. 2003). Among the most common sponge species reported in the area there are *Crambe crambe* (Schmidt, 1862), *Phorbas* sp., *Chondrilla nucula* Schmidt, 1862, *Sarcotragus* spp., *Ircinia* spp., and *Cliona* spp. (Guidetti et al. 2003).

Sampling design and collection of data

Data were collected at three depths (3 m, 5 m, and 7 m) along two belt transects (50 m long) in each of the two study sites. Within each transect, 10 photo-quadrats (0.25 m^2, a few meters apart) were taken at random using a Nikon AW130 camera. The Image-J software package was used to estimate the percentage cover of all sessile species present. Samples of sponges were collected for taxonomic identification and fixed in 80% ethanol. Skeleton and spicule preparations were made using standard methods (Rützler 1978). The taxonomic identification was based on Systema Porifera (Hooper and Van Soest 2002), Fauna d'Italia (Pansini et al. 2011), and the World Porifera Database (WPD) (Van Soest et al. 2019).

Due to the indistinguishable external morphology of some specimens, it was necessary to combine some species into operational taxonomic units (OTUs), such as 'black massive sponges' (BMS), which included *Spongia officinalis*, *Sarcotragus spinosulus*, and *Ircinia variabilis*; the 'encrusting red sponges' morphological group (ERS) counted *Crambe crambe*, *Phorbas fictitius* (Bowerbank, 1866), *Clathria (Microciona)* sp., *Hymeniacidon perlevis* (Montagu, 1814), and *Hemimycale columella* (Bowerbank, 1874). OTUs as morphospecies are known to be generally effective for the identification of patterns of distribution of benthic invertebrates (Brind'Amour et al. 2014), marine sponges in particular (De Voogd and Cleary 2008; Schlacher et al. 2010; Downey et al. 2018), at the same time avoiding the need for destructive sampling in concerned habitats.

Statistical analysis

Permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) based on Bray-Curtis untransformed dissimilarities was used to examine differences in assemblage structure among depths and transects, separately for each site. The analysis was based on a two-way model including the crossed factors 'Depth' (fixed, three levels: 3 m, 5 m, 7 m) and 'Transect' (random with two levels), with the ten photo-quadrats sampled in each transect providing the replicates. When relevant, paired *t* tests were done for post-hoc comparisons of significant multivariate differences between depths.

Multivariate patterns of 'average' assemblages in each combination of transect and depth, separately for each site,

Table 1 Summary of the taxonomic analysis of the sponges recorded during the study (* red encrusting sponges; ** black massive sponges)

Class	Subclass	Order	Species
Demospongiae	Heteroscleromorpha	Clionaida	*Cliona schmidtii* (Ridley, 1881)
			Cliona viridis (Schmidt, 1862)
		Poecilosclerida	*Crambe crambe* (Schmidt, 1862) *
			Hemimycale columella (Bowerbank, 1874) *
			Phorbas fictitius (Bowerbank, 1866) *
			Clathria (Microciona) sp. *Schmidt*, 1862 *
		Suberitida	*Hymeniacidon perlevis* (Montagu, 1814) *
	Verongimorpha	Chondrillida	*Chondrilla nucula* Schmidt, 1862
		Chondrosida	*Chondrosia reniformis* Nardo, 1847
		Verongiida	*Aplysina aerophoba* (Nardo, 1833)
	Keratosa	Dictyoceratida	*Ircinia variabilis* (Schmidt, 1862) **
			Ircinia sp. Nardo, 1833 **
			Sarcotragus spinosulus Schmidt, 1862 **
			Spongia officinalis Linnaeus, 1759 **

were visualised by non-metric multidimensional scaling (nMDS) based on Bray-Curtis untransformed dissimilarities. The SIMPER procedure (Clarke 1993) was used to quantify the absolute (δ_i) and the percent (δ_i %) contribution of each taxon to the total dissimilarity between depths, using a cut-off of 90% of cumulative dissimilarity for excluding low contributions.

Data on the percentage cover of each sessile taxon identified as relevant by SIMPER were analysed with analysis of variance (ANOVA) based on the same model as that used for PERMANOVA. When relevant, the 'Depth x Transect' term was eliminated from the linear model to test for the effect of 'Depth', according to Winer et al. (1991) and Underwood (1997). Before each ANOVA, the assumption of homogeneity of variances was checked with Cochran's C test. Log transformation of the data was performed when necessary. When heterogeneity of variances could not be removed by transformation, untransformed data were analysed and non-significant results (at $p > 0.05$) were considered robust as the probability of Type II error is not affected by heterogeneity of variances (Underwood 1997). The Student-Newman-Keuls test was used for post-hoc comparisons between depths, when relevant.

Results

Assemblage description

The benthic assemblages at both sites were characterised by a large abundance of sponges and ephemeral algae (see Appendix 1). Site 1 had the highest abundance of sponges over the barren substrate, with a mean cover ranging from 11% to 33% and maximum values in some quadrats up to 85%. In site 2, the abundance of sponges was slightly lower, with mean cover of 3–30%, although patches with a high sponge density (up to 78%) were found. The taxonomic survey resulted in the identification of 14 sponge taxa, 12

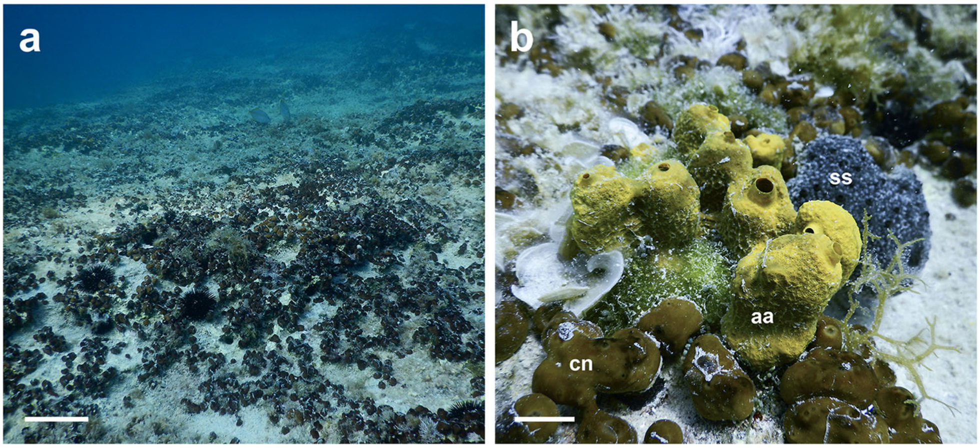

Fig. 2 Photographs of the benthic assemblages. **a** General view of the sponge ground at site 1 Santa Caterina, transect 2 at 5 m of depth; **b** close-up of some of the most abundant species found in this study, such as cn *Chondrilla nucula,* ss *Sarcotragus spinosulus* and aa *Aplysina aerophoba*

Table 2 Permutational multivariate analysis of variance (PERMANOVA) and pairwise tests comparing shallow subtidal sponge-dominated assemblages among three depths (3 m, 5 m, and 7 m) in each of two transects from two sites along the Apulian coast. Significant effects are indicated in italics

Source of variation	df	MS	pseudo-F	p
Site 1				
Depth = De	2	2285.1	1.69	0.129
Transect = Tr	1	35,281.0	26.05	*0.001*
De × Tr	2	8939.3	6.60	*0.001*
Residual	54	1354.5		
Pairwise tests for De × Tr:	Transect 1		Transect 2	
	3 m = 5 m ($t = 1.45$, $p = 0.072$)		3 m = 5 m ($t = 1.44$, $p = 0.071$)	
	3 m = 7 m ($t = 1.28$, $p = 0.188$)		*3 m ≠ 7 m* ($t = 3.17$, $p = 0.002$)	
	5 m ≠ 7 m ($t = 1.75$, $p = 0.021$)		*5 m ≠ 7 m* ($t = 2.32$, $p = 0.020$)	
Site 2				
Depth = De	2	12,213.0	6.99	*0.001*
Transect = Tr	1	5324.0	3.05	*0.028*
De × Tr	2	5073.6	2.90	*0.007*
Residual	54	1746.8		
Pairwise tests for De × Tr:	Transect 1		Transect 2	
	3 m ≠ 5 m ($t = 2.02$, $p = 0.005$)		3 m = 5 m ($t = 1.81$, $p = 0.052$)	
	3 m ≠ 7 m ($t = 2.88$, $p = 0.001$)		*3 m ≠ 7 m* ($t = 2.63$, $p = 0.001$)	
	5 m = 7 m ($t = 0.94$, $p = 0.425$)		*5 m ≠ 7 m* ($t = 2.89$, $p = 0.002$)	

identified at the species level and 2 at the genus level (Table 1). The most abundant sponge species was *C. nucula*, which accounted for 26–96% and 0–76% of the total sponge cover in site 1 and site 2, respectively. The second most abundant sponge taxon was the BMS, which reached cover values of 0.04–3.9% and 0–5.9% in site 1 and site 2, respectively. At site 1, none of the other sponge species exceeded 1% of cover, while at site 2 a considerable cover contribution was provided by *Aplysina aerophoba* (mean cover: 0.02–3.9%), *Cliona viridis* (mean cover: 0.09–2.0%), and *Ircinia variabilis* (mean cover: 0–1.3%).

Among algae, the most abundant were the filamentous turf-forming green algae (hereafter indicated just as turf), with a mean cover of 5–76%, followed by *Padina pavonica* (0.2–44%) and *Amphiroa* sp. (0.02–10%). A considerable proportion of the substrate, however, was characterised by bare rock (2–58%). Sea urchins did not generally exceed 10 individuals/m^2. The only exception was transect 2 of site 1 at 3 m depth, where the abundance of urchins reached 19 individuals/m^2 (see Appendix 3). It is worth noting that sponges and algae appeared patchily and inversely distributed: areas with high coverage of sponges alternated with areas characterised by relatively more abundant algae (Fig. 2).

Multivariate structure of assemblages

At both sites, the structure of sponge assemblages (combining both the identity and the relative abundance of constituent taxa) varied depending on the combination of depths and transects (Table 2). At site 1 (Santa Caterina), assemblages differed between 3 and 7 m depth in transect 2 and between 5 and 7 m depth in both transects. At site 2 (Porto Cesareo), they differed between 3 and 5 m depth in transect 1, between 3 and 7 m depth in both transects, and between 5 and 7 m depth in transect 2. No significant differences were found in all other combinations of depths and transects (Table 2). These multivariate patterns were graphically evident in terms of both a spatial separation and a different dispersion of centroids corresponding to the different combination of levels of the examined factors in the nMDS plots (Fig. 3a, b).

Abundance of individual taxa

Overall, five sessile taxa were identified as contributing most to differences between depths at each site. These included the sponges *C. nucula* and BMS, the brown alga *P. pavonica*, algal turf, and the calcareous red alga *Amphiroa* sp. (see Appendix 2).

At Santa Caterina (site 1), in particular, the abundance of both *C. nucula* and *P. pavonica* did not vary among depths, although the first species was heterogeneously distributed between transects independently of depth (Table 3 and Fig. 4a, b). Both *P. pavonica* and turf were affected by the combination of depths and transects (Table 3), although with contrasting patterns. Along transect 1, *P. pavonica* was comparably abundant at all depths, while along transect 2, it progressively decreased with the reduction of depth (Fig. 4c). The cover of turf, instead, was larger at 7 m than at 5 m depth along transect 1, and larger at 3 m compared with 7 m depth along transect 2, with the third examined depth being inconsistently ranked between the other two in both transects (Fig. 4d). Finally, a main effect of 'Depth' was detected for *Amphiroa* sp., which showed consistently larger abundance at 5 m compared with 3 m and 7 m depth. This result should be interpreted with caution due to a significant violation of the assumption of homogeneity of variances (Table 3). The graphs, however, confirmed that the pattern was not critically biased by heteroscedasticity (Fig. 4e).

At Porto Cesareo (site 2), almost all relevant sessile taxa (*Chondrilla nucula*, BMS, turf, and *Amphiroa* sp.) varied interactively with depths and transects, with the only exception being *P. pavonica* that did not show any significant differences between depths or transects (Table 4 and Fig. 5a–e). Specifically, *C. nucula* was more abundant at 3 m than at 5 m and 7 m depth along transect 1, while it did not vary with depth along transect 2 (Fig. 5a). The BMS were similarly abundant across depths in transect 1, while the cover of this taxon was larger at 5 m compared with the two other sampled depths along transect 2 (Fig. 5b). Comparable abundance among depths was shown by turf and *Amphiroa* sp. along transect 1 and transect 2, respectively. Along transect 2, the cover of turf was larger at 5 m compared with 7 m depth (with no alternative hypothesis for 3 m depth: Fig. 5d), while *Amphiroa* sp. was more abundant at 3 m compared with both the other depths (Fig. 5e).

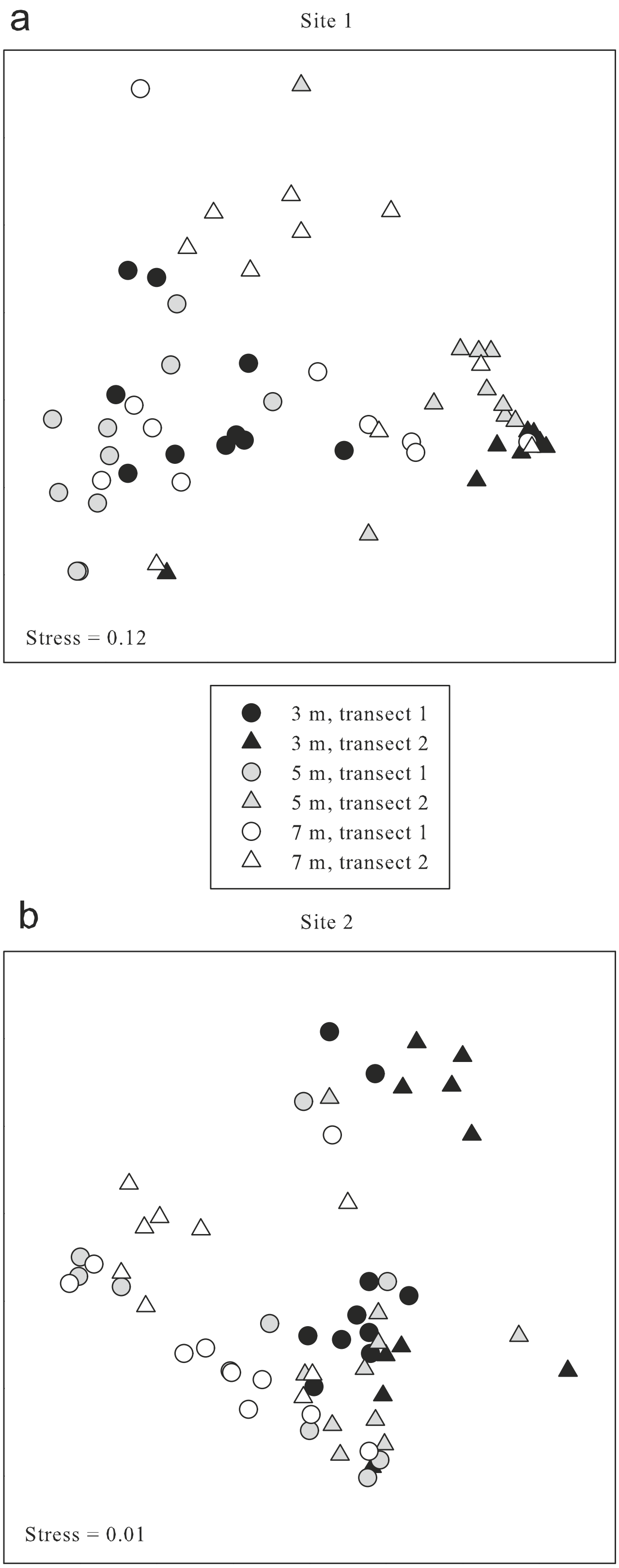

Fig. 3 nMDS plots comparing shallow subtidal assemblages at three depths and two transects from each of two sites along the Apulian coast. Each symbol is the 'average sample' in each of ten replicate quadrats

Discussion

This study represents the first taxonomic and quantitative characterisation of a shallow-water light-exposed sponge ground in the Mediterranean Sea. The faunal lists available for the western coast of the Salento Peninsula indicate that the structure of the present sponge ground matches to a large degree the typical species composition of Mediterranean rocky subtidal and barren habitats (Corriero et al. 1984; Parenzan 1984; Corriero et al. 2004; Costa et al. 2018; Longo et al. 2018).

The distinctiveness of the present assemblages is represented by the spatial dominance of sponges that were observed to occupy up to 85% of the substratum, with a mean percentage cover up to 33% along 50 m transects. This abundance is very unusual for the Mediterranean Sea, where shallow and relatively sheltered rocky shores are commonly dominated by macroalgae (Pérès and Picard 1964; McQuaid and Branch 1985; Kraufvelin et al. 2010). At both study sites, sponge aggregations were grouped between 3 and 7 m depth and were mainly constituted by *C. nucula* and "black massive sponges".

The dominant sponge species within the examined assemblages, however, was *C. nucula*. This photophilous species hosts photosynthetic cyanobacteria and contains toxic chemical compounds that make it a strong competitor for space,

Table 3 Results of analysis of variance (ANOVA) on the abundance (percentage cover) of single taxa from shallow subtidal assemblages from site 1 along the Apulian coast

Source of variation	df	*Chondrilla nucula*		Black massive sponges		*Padina pavonica*		Turf		*Amphiroa* sp.	
		MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Depth	2	134.5	0.19	37.86	5.45	6.55	0.44	1316.1	0.25	19.33	3.79*[a]
Transect	1	1920.4	4.54*	22.18	2.56	5.94	3.63	20,214.7	32.73***	5.07	0.99
Depth × Transect	2	709.5	1.68	6.95	0.80	14.92	9.11***	5332.1	8.63***	3.30	0.65
Residual	54	423.1		8.66		1.64		617.6		5.10	
Cochran's test		*C* = 0.279		*C* = 0.557**		*C* = 0.328		*C* = 0.297		*C* = 0.715**	
Transformation		None		None		Ln(x + 1)		None		None	

[a] Tested over the Residual MS after elimination of the Depth × Transect term that was not significant with $p > 0.25$

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

without reported predators in the Mediterranean Sea (Vicente 1990; Arillo et al. 1993; Milanese et al. 2003). In general, *C. nucula* was patchily distributed on the seafloor. This sponge, however, had a similar distribution across depths and transects at site 1, while it was relatively more abundant at 3 m depth at site 2, but only along transect 2. These results agree with previously reported evidence that composition of sponge assemblages is shaped by factors acting at small scales (Bell 2007). Wave exposure is another factor that can affect the composition of benthic communities (Sebens 1991). In Santa Caterina (site 1), in particular, transect 2 was located northward of transect 1. Here, transect 2 showed a larger abundance of both the seasonal alga *P. pavonica* and the BMS compared to transect 1. This pattern could be driven by the effect of the prevalent coastal winds that, in the Salento Peninsula, blow from north-east (Mangia et al. 2004), potentially making the two transects subject to different hydrodynamic and sedimentation regimes. Such environmental factors are known drivers of variation of benthic assemblages in general (Rosenberg 1995; Guichard and Bourget 1998; Airoldi 2003), and sponge assemblages in particular (Sebens 1991; Bell and Barnes 2000).

In tropical areas, the occurrence of shallow-water sponge grounds has been mainly associated with environmental deg-

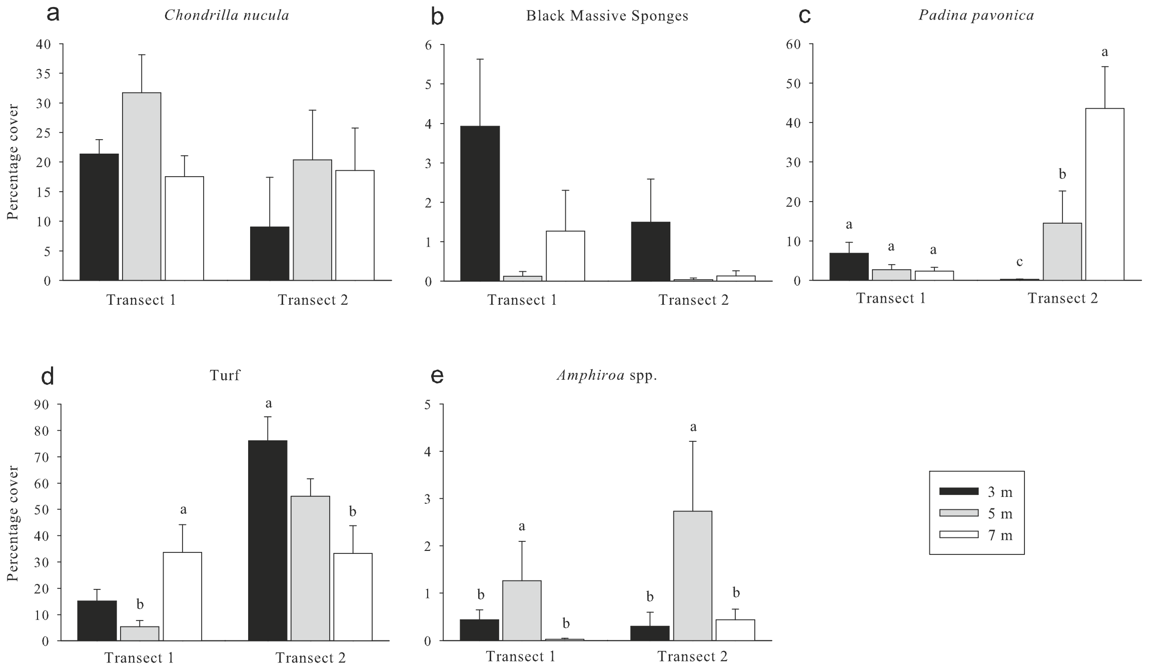

Fig. 4 Mean (+ SE, $n = 10$) abundance of individual taxa, illustrating differences between depths and transects at site 1. Different letters above bars represent means differing significantly at $p < 0.05$ (SNK tests). Only comparisons within each transect are appropriate in c and d. Note that different graphs are on different scales

Table 4 Results of analysis of variance (ANOVA) on the abundance (percentage cover) of single taxa from shallow subtidal assemblages from site 2 along the Apulian coast

Source of variation	df	*Chondrilla nucula*		Black massive sponges		*Padina pavonica*		Turf		*Amphiroa* sp.	
		MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Depth	2	20.99	5.05	1.76	0.55	7158.8	4.52	939.8	0.29	138.66	0.91
Transect	1	3.65	2.47	4.43	8.12**	2200.6	3.92	235.1	0.25	23.44	2.86
Depth × Transect	2	4.16	2.82*	3.19	5.85**	1584.0	2.82	3256.6	3.42*	152.44	18.61***
Residual	54	1.48		0.55		562.1		951.9		8.19	
Cochran's test		$C = 0.334$		$C = 0.362$		$C = 0.410$		$C = 0.272$		$C = 0.358$	
Transformation		$\mathrm{Ln}(x+1)$		$\mathrm{Ln}(x+1)$		None		None		None	

$^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$

radiation and coral decline due to extreme thermal events and other anthropogenic impacts (Bell and Smith 2004; Kelmo et al. 2013; Maldonado et al. 2017).In the Caribbean Sea, for instance, a species of *Chondrilla* rapidly increased in abundance and became dominant in the reef after thermal anomalies due to the 1998 El Niño event that had caused severe bleaching and mass mortality of corals (Aronson et al. 2002). *Chondrilla* remained the dominant component on the substratum for 10 years, until 2009 when an earthquake killed almost all the organisms in the area (Norström et al. 2009; Aronson et al. 2012).

The domination of *C. nucula* in the present Apulian study system is consistent with such observations, although in a different environmental and biological context. To the best of our knowledge, no historical quantitative data are available for the area examined in our study. According to the earliest naturalistic studies made in the area, however, the shallow rocky reefs were reported to be characterized by photophilous macroalgae (Solazzi 1967 and 1968; Parenzan 1973 and 1983). More recently, the whole Salento Peninsula was affected by the heavily destructive date-mussel fishery that originated persistent barren habitats (Russo and Cicogna 1991; Fanelli et al. 1994; Guidetti et al. 2003; Bonaviri et al. 2011; Guidetti 2011). Our area of study was found to be one of the most heavily damaged (Fanelli et al. 1994). Under such circumstances, it is plausible that sponges took advantage of the increased availability of free space. Indeed, the sea urchins *Arbacia lixula* and *Paracentrotus lividus* are common at the study sites and are known to feed intensely on algae and other invertebrates such as bryozoans, hydrozoans, barnacles, and polychaetes (Privitera et al. 2008; Wangensteen et al. 2011). Sponges are known to compete for the substrate with other

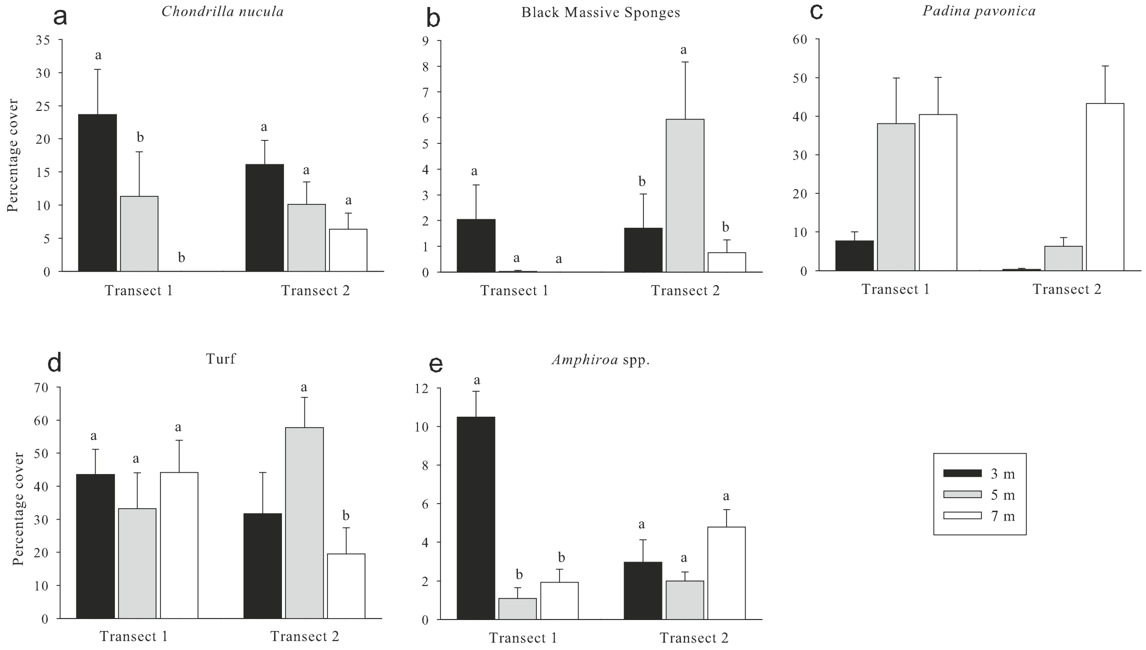

Fig. 5 Mean (+ SE, $n = 10$) abundance of individual taxa, illustrating differences between depths and transects at site 2. Different letters above bars represent means differing significantly at $p < 0.05$ (SNK tests). Only comparisons within each transect are appropriate in a, b, d, and e. Note that different graphs are on different scales

sessile organisms (Dayton et al. 1974; Jackson and Buss 1975). However, especially on moderately exposed rocky shores of temperate seas, macroalgae are among the strongest space occupiers (Palumbi 1985; Davis et al. 1997; Cebrian and Uriz 2006; Baldacconi and Corriero 2009; Cárdenas et al. 2016). Therefore, it is likely that their anthropogenic removal could trigger the dominance by sponges.

Furthermore, a comparison with data from 2002, shortly after the ban of the *L. lithophaga* fishery, seems to indicate a reduction of sea urchins and of the percentage cover of bare substrate. At La Strea, Porto Cesareo (close to transect 1 at site 2), between 5 and 7 m depth, an average of ~ 20 sea urchins per m^2 was reported in 2002 (Guidetti et al. 2003). Fifteen years later, we found an average of just two urchins per m^2. This reduction may be associated with the reduction in the percentage of bare substrate, which changed from 90 to 95% in 2002 (Guidetti et al. 2003) to 11–14% in 2017. Such drastic ecological change may explain the large occurrence of ephemeral and seasonal algae, typical of impacted and urbanized environments, in the assemblage described here (Hay 1981; Piazzi et al. 1999; Benedetti-Cecchi et al. 2001; Bulleri et al. 2002).

In addition to biological interactions, ocean warming associated with global change could have provided a further contribution to the establishment of the examined sponge ground. Thermal anomalies have already led to mass mortality events and species shifts in the Mediterranean Sea and worldwide (Coma et al. 2009; Hoegh-Guldberg and Bruno 2010; Rivetti et al. 2014). Recent studies indicate that certain sponge species are less sensitive to ocean warming and acidification compared with many other benthic organisms (Bell et al. 2013). Therefore, they could benefit from environmental conditions related to global change compared with other organisms (Bell et al. 2018b). This type of evidence is available also for the eastern Mediterranean Sea (Bianchi et al. 2014). Furthermore, Bertolino et al. (2017a, b) suggest that, on a millennial time-scale, seawater warming coincides with changes in sponge assemblage composition and an overall increase of sponge richness.

Therefore, there are reasons to believe that the assemblages reported in this study would represent not just an isolated and temporary phenomenon, but also an important early-warning indicator of a future scenario in temperate shallow subtidal environments similarly to impacted coral reef systems (Bell et al. 2018a). However, manipulative experiments are necessary to unambiguously test for the previously discussed models and hypotheses. These must be specifically designed to unravel the causal role of biotic and abiotic factors and their possible interactions that allow the formation and the plausible persistence of these shallow-water sponge grounds. In conclusion, information from studies such as the present one, possibly expanded to larger spatial and temporal scales (Dayton et al. 2016), is essential to guarantee that effective measures include a representative sample of target organisms, of their natural variability, and of the responsible factors even if not yet fully known (Benedetti-Cecchi et al. 2003).

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Compliance with ethical standards

Ethical approval All applicable international, national, and institutional guidelines for animal testing, animal care, and use of animals were followed by the authors.

Conflict of interest The authors declare that they have no conflict of interest.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements. The study is compliant with CBD and Nagoya protocols.

Data availability All data generated or analysed during this study are included in this published article.

Author Contribution FS, VM and MB conceived and designed research. FS and VM conducted field samplings and wrote the manuscript. GC collected qualitative and quantitative data from photo-quadrats and trough taxonomic identification of sponge species. IB contributed to the experimental design and to the statistical analysis. All authors contributed, read and approved the manuscript.

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