MEDITERRANEAN MARINE CAVES: REMARKABLE HABITATS IN NEED OF PROTECTION

MedKeyHabitats II project

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FOREWORD

Underwater caves are "natural cavities big enough to permit direct exploration by man". Dark underwater caves are lightless enclaves of the marine environment, with lighting less than 0.01% and a fairly confined space, are often reservoirs of unknown biodiversity and refuges for generally very non-resilient communities. Underwater caves are specific entities easily accessible because of their often-shallow depth and their nearness to the coast. Also, the caves, at least in their "semi-dark" parts, constitute landscapes of high aesthetic or archaeological value and are therefore often visited, leading to mechanical harm particularly from divers. Using destructive methods (e.g. dynamite) in coastal development work is likely to significantly affect these habitats.

Underwater caves are particularly well represented in all the rocky karst or fractured coastlines and are probably very widespread at Mediterranean level. Although we do not have an exhaustive view of the situation, the Parties to Barcelona Convention adopted in 2013, the Regional Action Plan commonly named "Dark Habitat Action Plan[1]" to:

- Conserve the habitats' integrity, functionality (favourable state of conservation) by maintaining the main ecosystem services (e.g. carbon sink, halieutic recruitment and production, biogeochemical cycles) and their interest in terms of biodiversity (e.g. specific diversity, genetics),

- Encourage the natural restoration of degraded habitats by reducing human impacts,

- Improve knowledge about dark populations (e.g. location, specific richness, functioning, typology).

Although scientific knowledge on dark habitats has increased during the last decades, there is still a significant gap today and the scarcity of information on the current state of these habitats (distribution, density of key species, etc.) due to (i) the high cost and difficulties for accessing, and (ii) the lack of historic data and time series.

This document aims to establish a first review of the recent available data regarding marine caves distribution, biodiversity, ecosystem structure and functioning, dynamics, ecological status, impact and management potential. It is also a collaborative work to which all the Contracting Parties have contributed through internal consultations.

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[1] Action Plan for the conservation of habitats and species associated with seamounts, underwater caves and canyons, aphotic hard beds and chemosynthetic phenomena in the Mediterranean Sea

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Semi-submerged tunnel in Saria Island, Greece.
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1. MARINE CAVES & CAVE SPECIES

The term "cave" is commonly used to describe an opening from the surface into a natural underground or underwater hollow, which can be penetrated by humans (Gunn, 2004; Romero, 2009). Caves can be horizontal, vertical, or a combination of both, and their long dimension (i.e. length or depth) is greater than the cross-sectional dimensions at the entrance (Gunn, 2004; Gerovasileiou *et al.*, 2016b). They are formed by different processes in various rock types (e.g. carbonate or volcanic). Most caves are formed due to the dissolution of bedrock by water circulating through fissures and pores (known as *solution* or *karst caves*) while marine caves (also known as *littoral* or *sea caves*), are usually formed due to wave action abrasion (Riedl, 1966; Cicogna *et al.*, 2003; Gunn, 2004). Thus, different classification schemes and terminologies exist with regard to their origin and formation process (*speleogenesis*), type of host rock and water regime, while local terms exist in several cases (e.g. "Vrulja" in Croatia for underground streams discharging under the sea level - see Surić *et al.*, 2010). According to Bianchi *et al.* (1996), the phrase *marine cave* defines a cavity of various origins, entirely or partly occupied by the sea, accessible to man, which has significant horizontal and volumetric development: a possible criterion is that the ratio between the numbers expressing the total volume (in m^3) and the entrance area (in m^2) must be greater than 1, and that the width of the entry must not exceed the internal average.

Recently, a standard glossary, based on existing terminology for marine and anchialine[1] cave systems and their biota, was developed by the Editorial Team of the World Register of marine Cave Species (WoRCS) database (see Gerovasileiou *et al.*, 2016b). Marine caves can be further assigned to three main categories according to their submersion level: (a) submerged, extending below the water level; (b) semi-submerged, extending - at least partly - at the level of the water surface; and/or (c) intertidal, which are exposed to and affected by sea surface dynamics. The cave morphology can be also variable, with the most conspicuous types being *blind-ended* caves (ending as a cul-de-sac), *tunnels* (opening to entrances at two or more ends), *pits* (vertical cave with negligible horizontal passages) or more complex morphologies (consisting of arrays of intersecting passageways that form distinctive patterns) (Riedl, 1966; Palmer, 1991; Field, 1999; Gerovasileiou *et al.*, 2016b).

Aquatic cave biota can be assigned to four main ecological categories (Culver & Pipan, 2009; Romero, 2009; Culver & White, 2012; Gerovasileiou *et al.*, 2016b): (a) *stygobionts* (or cave-exclusives *sensu lato*),

which are obligatory aquatic cavernicoles, adapted to subterrainean life (e.g. loss of pigmentation and vision); (b) *stygophiles*, aquatic species that can live and complete their life cycle within caves, but can also be found in suitable habitats outside caves (e.g. undersides of rocks, deep waters); (c) *stygoxenes*, aquatic species which occur in caves, but do not complete their life cycle within caves, and periodically move outside (e.g. finding shelter within caves during daytime but looking for food sources in nearby external habitats during night); (d) *accidental* (or random visitors), which may enter caves by chance (e.g. drifted by currents or become disoriented and lost), but can only survive in this environment for short periods of time.

Marine caves harbour a diverse biota (see chapter 8). In contrast to terrestrial caves, they are not "sufficiently" isolated from the external environment due to the continuity of the aqueous medium (Bianchi *et al.*, 1996). Thus, the majority of species recorded in this habitat type could be characterized as stygophiles (e.g. sponges and bryozoans which also occur in dimly lit environments outside caves, such as coralligenous reefs and deeper waters) or stygoxenes (e.g. crustaceans and fish exhibiting nychthemeral movements inside-outside caves for feeding) (Riedl, 1966; Harmelin *et al.*, 1985; Balduzzi *et al.*, 1989; Bianchi *et al.*, 1996; Bussotti *et al.*, 2018). This dominance of cryptobiotic (i.e. preferring cryptic habitats) and bathyphilic species in marine caves has been also characterized as "secondary troglobiosis" (Cattaneo & Pastorino, 1974), since these species originate from external environments but are also very characteristic of marine caves. Nonetheless, a considerable number of taxa have not been – at least yet – reported from other types of habitats, and thus, they could be characterized as cave-exclusive in the broad sense (although future research, for instance in cryptic and deep-sea habitats, could reveal the opposite) (Gerovasileiou & Voultsiadou, 2012). Over the last years, the scientific exploration of underwater caves, and especially those of the anchialine type, has led to outstanding discoveries of novel taxa which exhibit unique adaptive features to cave life (Iliffe *et al.*, 1983; Stock, 1994; Iliffe & Kornicker, 2009; Gerovasileiou *et al.*, 2016b and references therein). It is possible that some of these taxa are the result of ecological specialization from generalist ones which penetrated caves from external environments in the past, including "relict species" or palaeoendemics (e.g. remnants of the subtropical/tropical fauna which thrived in the Mediterranean Sea during warm periods of its history), which found refuge and survived in cave habitats (Harmelin *et al.*, 1985; Pérez *et al.*, 2004).

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[1] The term "anchialine" or "anchihaline" derives from the Greek word "αγχίαλος" (= near the sea) and is used to characterize localities/habitats hosting water bodies with marine origin, but restricted exposure to open air, as well as negligible exchange with the open sea by diffusion with contiguous marine water bodies, through more or less extensive subterranean connections (Stock *et al.*, 1986; Gerovasileiou *et al.*, 2016b). The marine "marginal caves" ("Randhöhlen" in Riedl, 1966 and Riedl & Ozretić, 1969), which are also characterized by a subterranean connection to the sea and contain mixohaline water bodies, fall within the category of anchialine caves (Stock *et al.*, 1986).

Speleothems in a semi-submerged cave.
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2. DISTRIBUTION

Rocky substrates constitute more than half (54%) of the Mediterranean coastline (Stewart & Morhange, 2009) with limestone being one of their most characteristic components (Lewin & Woodward, 2009). Through time, the ongoing geodynamic processes (e.g. karstic phenomena) in this semi-enclosed sea have resulted in the formation of a high number of more or less complex marine and anchialine cave systems (Gerovasileiou & Voultsiadou, 2012). According to the latest census by Giakoumi *et al.* (2013), approximately 3,000 marine caves (semi- and entirely submerged) have been recorded in the Mediterranean basin to date (Fig. 2.1). Most of these caves (97%) are located in the North Mediterranean, which encompasses a higher percentage of carbonate rocky coasts and has been more extensively studied for this particular habitat type (see next chapter). Specifically, the highest numbers of known marine caves are located in the Eastern Adriatic, Aegean, Tyrrhenian, Provencal and Ionian coasts (Table 2.1), where they are sometimes densely concentrated in insular areas and rocky peninsulas (e.g. Aegean Archipelago, Croatian and Balearic Islands, and Corsica). At local or regional scales, detailed mapping initiatives have taken place in Italy (Cicogna *et al.*, 2003), Corsica (CREOCEAN-DREAL, 2010), Croatia (Surić *et al.*, 2010) and Greece (Sini *et al.*, 2017). In addition, expeditions in the framework of the research projects MedKeyHabitats, MedMPAnet and LIFE BaҤAR for N2K have recently provided information on the distribution of this habitat type in previously understudied Mediterranean areas (see case studies below). However, given the logistic constraints involved in the inventorying of underwater caves, and especially the submerged ones, their number is assumed to be much higher at both Mediterranean and regional scales, and mapping efforts are required in order to fill current distribution gaps in the Eastern and Southern Mediterranean regions. Detailed guidelines for the inventorying of dark habitats, including marine caves, have been recently provided by SPA/RAC-UN Environment/MAP & OCEANA (2017).
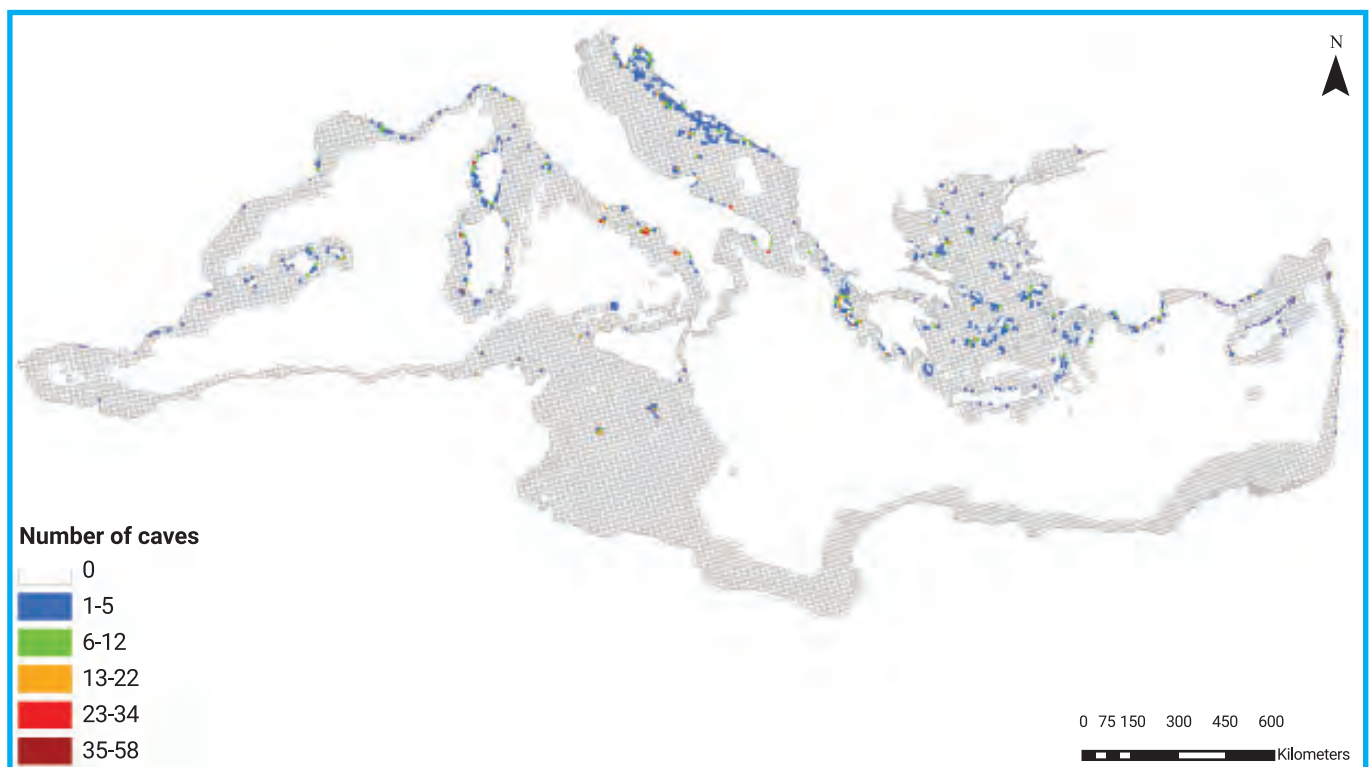
Fig. 2.1. Distribution of marine caves in the Mediterranean Sea. Different colours indicate the number of caves recorded in cells of 10 x 10 km (from Giakoumi *et al.*, 2013).

The majority of existing marine cave records correspond to shallow and/or semi-submerged caves, with a depth that rarely exceeds 15 m, which are generally easier to spot and access by both scientists and recreational divers. Information about deeper caves in the existing scientific and grey literature is limited, with only a small number of marine caves studied for their biota, having a maximum depth of 30-40 m (Gerovasileiou & Voultsiadou, 2012). However, in several cases bathymetric data are lacking. The recent study of deeper areas with the use of Remotely Operated Vehicles (ROVs) has shown that hard substrates in deeper waters can also bear large overhangs and cavities. For instance, deep-water caves and large overhangs have been recently discovered in the Linosa Trough (Freiwald *et al.*, 2009)

and west of Gozo, at depths of 270-795 m, possibly dating back to the Messinian (Evans *et al.*, 2016; Borg *et al.*, 2017). However, their study involves several limitations as a result of operational difficulties and constitutes a challenge for future explorations.

Table 2.1. Number of marine caves recorded by Mediterranean ecoregion
(according to Giakoumi *et al.*, 2013; Sini *et al.*, 2017 and data from case studies – see Box 2.1 below).

MEDITERRANEAN ECOREGION	NUMBER OF MARINE CAVES
Alboran Sea	24
Algero-Provencal Basin	459
Tyrrhenian Sea	581
Tunisian Plateau/Gulf of Sidra	68
Adriatic Sea	708
Ionian Sea	307
Aegean Sea	622
Levantine Sea	209

Box 2.1. Case studies

During the last years, research expeditions and baseline studies in the framework of the scientific projects MedMPAnet, MedKeyHabitats and LIFE BaĦAR for N2K have provided valuable information on the distribution of the marine cave habitat, its biodiversity and threats in understudied regions of the Mediterranean Sea. For example, a number of caves, tunnels and numerous small caverns were recorded in Cap des Trois Fourches and Jbel Moussa, in Morocco (CAR/ASP-PNUE/PAM, 2012, 2013; UICN, CAR/ASP & HCEFLCD, 2014; PNUE/PAM-CAR/ASP, 2016b) and in Île de Rachgoun, in Algeria (PNUE/PAM-CAR/ASP, 2016a).

Marine caves and tunnels in these areas were found to harbour rich benthic assemblages, including many protected species (e.g. the anthozoans *Astroides calycularis* and *Corallium rubrum* and the sponge *Spongia lamella*). In Lebanon, Raoucheh Cave and other caves in Ras Chekaa and Nakoura areas were studied within MedMPAnet project (RAC/SPA-UNEP/ MAP, 2012, 2013b, 2014). These caves were found to host among the richest filter-feeding assemblages in the whole region, including sponges so far endemic to this area and habitats (e.g. the horny sponge *Euryspongia raouchensis*, the lithistids *Gastrophanella phoeniciensis* and *Microscleroderma lamina*, an unknown *Aplysina* and undescribed axinellids). It is also worth noting that several non-indigenous species of Indo-Pacific origin were found in marine caves of Lebanon (e.g. the crab *Charybdis helleri*, the ascidians *Symplegma brakenhielmi* and *Phallusia nigra* and the fishes *Pempheris rhomboidea* and *Sargocentron rubrum*).

Within MedMPAnet and MedKeyHabitats projects, marine caves were also recorded and studied in the Adriatic Sea, specifically, small midlittoral caves in Albania (RAC/SPA-UNEP/MAP, 2013a) and large marine caves in Platamuni area of Montenegro, which were dominated by scleractinian corals, sponges and erect bryozoans (UNEP-MAP-RAC/SPA, 2016a,b). More Recently, LIFE BaĦAR for N2K project shed light on numerous marine caves and tunnels of Malta and Gozo Islands (37 semi- and 52 fully submerged caves) of various sizes and depths, as well as 17 deep-water caves between 205 m and 795 m (Borg *et al.*, 2017). The projects and baseline studies mentioned above have significantly contributed to filling knowledge gaps in previously understudied marine regions, leading to the proposal and establishment of new Marine Protected Areas..
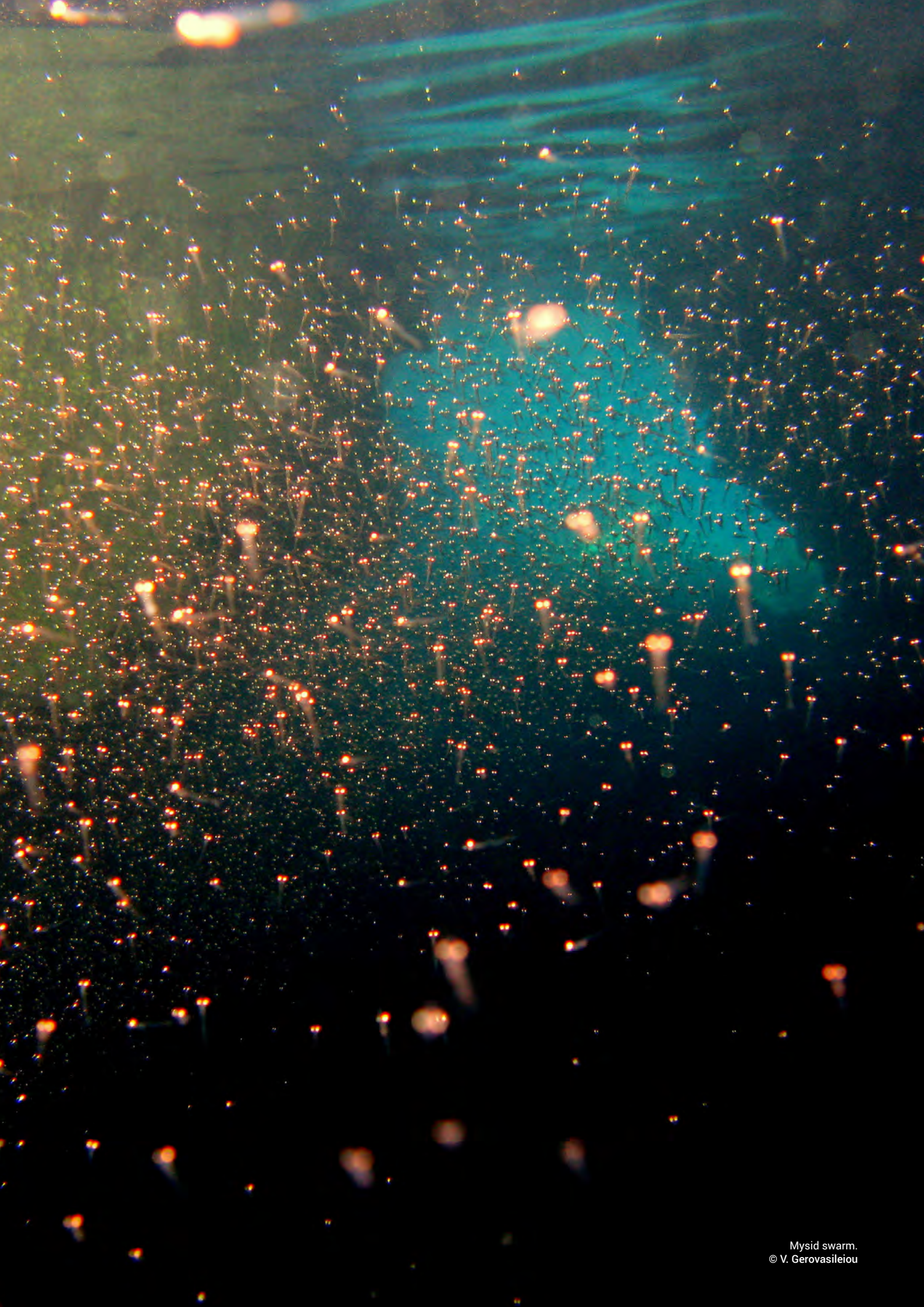
Mysid swarm.
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3. THE BIOLOGICAL STUDY OF MEDITERRANEAN MARINE CAVES

In contrast to terrestrial caves, their marine counterparts remained totally unexplored until the second half of the 20th century. Their study became possible only after the development of autonomous diving, which not only allowed cave exploration but also direct observation and sampling by marine scientists (Laborel, 1960; Vacelet, 1967). Technological advances in autonomous diving, from the development of the first open circuit self-contained underwater breathing apparatus in 1942-3 (Drach, 1948) to the modern closed-circuit rebreathers (Iliffe & Bowen, 2001) have triggered underwater cave research and brought to light unique faunal elements (e.g. Jaume & Boxshall, 2005; Iliffe & Kornicker, 2009).

In the Mediterranean basin, the first studies on marine caves and their biota were conducted by French (Pérès & Picard, 1949, 1951, 1955; Corroy et al., 1958; Laborel & Vacelet, 1958, 1959; etc.), Austrian (Starmühlner, 1955a,b; Abel, 1959; Banse, 1959; Riedl, 1959a,b,c,d,e,f; Russ & Rützler, 1959; Rützler, 1965; Riedl, 1966; etc.) and Italian scientists (e.g. Sarà, 1958, 1959a, 1961a,b, 1962b, 1968, 1974, 1978; Cattaneo & Pastorino, 1974; Cinelli et al., 1977; Cantone et al., 1979; etc.), followed by contributions by Spanish scientists in the 1980s (Bibiloni & Gili, 1982; Gili et al., 1982, 1986; Bibiloni et al., 1984; etc.), and Croatian scientists after 2000 (e.g. Arko-Pijevac et al., 2001; Bakran-Petricioli et al., 2007, 2012; Radolović et al., 2015; Petricioli & Bakran-Petricioli, 2019). Studies focused on marine caves from the Eastern Mediterranean basin were published more recently by Greek scientists (Gerovasileiou et al., 2015a and references therein).

A notable landmark in the history of Mediterranean marine cave research was the publication of the book "Biologie der Meereshöhlen" by the Austrian zoologist Rupert Riedl (1966), which provided a first synthesis consolidating existing knowledge, acquired in the 1950s and 1960s. Much of the information that was assembled until this period came from the "Tyrrhenia-Expedition", which started in 1952 and focused on marine caves mostly in the Tyrrhenian Sea. A total of 529 taxa which belonged to 32 major groups were recorded within this expedition (Riedl, 1966). Some decades later, important overviews on marine cave research were published in Italy (Bianchi, 2003; Cicogna et al., 2003) and the Eastern Mediterranean Sea (Gerovasileiou et al., 2015a), while Gerovasileiou & Voultsiadou (2012) and Bussotti et al. (2015) provided overviews on the marine cave sponge and fish fauna, respectively, at the Mediterranean scale.

3.1. Taxonomic studies

The first approach to the biological study of marine caves – likewise other habitats – was undoubtedly taxonomic, a necessary and indispensable step to conduct any other type of ecological investigation. From the very first stages of marine cave research it became evident that this peculiar habitat harbours several previously undescribed species (Sarà, 1958, 1959b; Vacelet & Lévi, 1958; Vacelet, 1959; Sarà & Siribelli, 1960; Rützler & Sarà, 1962). Until today, studies in Mediterranean marine and anchialine caves are continuously bringing to light new species from various taxonomic groups: Porifera (Vacelet & Boury-Esnault, 1982, 1996; Pulitzer Finali, 1983; Pansini, 1984, 1996; Voultsiadou-Koukoura & Van Soest, 1991; Voultsiadou-Koukoura et al., 1991; Bibiloni, 1993; Boury-Esnault et al., 1995; Corriero et al., 1996, 1997b; Bavestrello et al., 1997; Muricy et al., 1998; Pansini & Pesce, 1998; Vacelet & Pérez, 1998; Vacelet et al., 2000, 2007; Manconi et al., 2006; Pérez et al., 2011; Pisera & Vacelet, 2011; Reveillaud et al., 2012; Lage et al., 2018; 2019), Priapulida (Todaro & Shirley, 2003), Gastrotricha (Fregni et al., 1998), Copepoda (Riera et al., 1991; Carola & Razouls, 1996; Jaume & Boxshall, 1996; Jaume, 1997; Jaume et al., 1999; Krsinic, 2005), Decapoda (Fransen, 1991; Pretus, 1990), Mysida (Wittmann, 2004; Alcaraz et al., 1986), Polychaeta (Zibrowius, 1968; Fassari & Mòllica, 1991), Gastropoda (Warén et al., 1997), Tardigrada (Villora-Moreno, 1996), Bryozoa (Silén & Harmelin, 1976; Harmelin et al., 2007; Hayward, 1974; Rosso et al., 2019), Brachiopoda (Logan & Zibrowius, 1994), Chaetognatha (Casanova, 1986), and Pisces (Kovačić, 1999).

Moreover, the study of marine cave biota revealed that these peculiar habitats harbour "living fossils" (Vacelet & Lévi, 1958; Pérez et al., 2004; Manconi & Serusi, 2008) and deep-water species (Pouliquen, 1969; Vacelet et al., 1994; Harmelin, 1997; Harmelin & Vacelet, 1997), triggering more taxonomic and ecological studies. In addition to the biodiversity inventories, the notable small-scale environmental gradients in marine caves as well as their reflection on the spatial variability of biota became a subject of research from the first pioneer bionomic studies until today.

3.2. Bionomic descriptions

The typology and distribution of benthic communities in Mediterranean marine caves have been mostly studied by French, Austrian and Italian scientists. Specifically, the first description of the structure of marine cave communities was published by Pérès & Picard (1949), who studied Niolon cave (Marseille area, France) and noticed that macroalgae (mostly Rhodophyta), which dominated at the cave entrance zone, were gradually replaced by sessile animals inwards (up to 90% of the wall surface cover) due to the decrease of light. In addition, despite the shallow depth of this cave (6-12 m), some species which usually develop in deeper waters were present. Some years later, in their first bionomic descriptions from the North-western Mediterranean

basin, Pérès & Picard (1951, 1955) described a type of the coralligenous biocoenosis, which develops in marine caves, under the name "coralligène de grotte". At this time, marine cave communities were characterized as an "impoverished aspect" of the coralligenous biocoenosis while the differentiation of their fauna was attributed to the reduction of water movement and light and the development of a black ferromanganese oxides coating on their interior hard substrate (Vacelet, 1964).

The clear distinction of the marine cave biocoenoses from the (pre-)coralligenous[2], which often occurs at the cave entrance, was based on the dominance of sessile animals versus macroalgae (Vacelet, 1959; Laborel, 1960, 1961). Therefore, Laborel & Vacelet (1959) described two successive biocoenoses which develop in marine caves along a decreasing light gradient: (1) a transitional dim light zone where biotic cover decreases from 100% (at the outer zone) to 50%, with the most characteristic species being the sponges *Aplysina cavernicola*, *Petrosia ficiformis*, *Ircinia variabilis* and *Petrobiona massiliana*, and the scleractinian corals *Leptopsammia pruvoti*, *Caryophyllia inornata* and *Madracis pharensis*, and (2) a completely dark zone where the biotic surface cover decreased to 20% or less while the remaining bare rock surface is covered by a black coating of ferromanganese oxides[3]. This latter zone is dominated by serpulid polychaetes, sponges and scleractinians, while the ceiling is perforated by holes of the bivalve *Lithophaga lithophaga*.

A few years later, the influential "Nouveau manuel de bionomie benthique" by Pérès & Picard (1964) (see also Pérès, 1967), which summarized and updated the existing knowledge on Mediterranean benthic communities, described three distinct biocoenoses developing along the horizontal cave axis as follows: (1) the coralligenous biocoenosis (biocénose coralligène - C), which can often develop at the cave entrance[4], (2) the semi-dark cave biocoenosis (*biocénose des grottes semi-obscures* - GSO), which – in the absence of macroalgae – is dominated by sponges (e.g. *Agelas oroides*, *Aplysina cavernicola*, *Oscarella lobularis* and *Petrosia ficiformis*) and anthozoan facies (e.g. *Parazoanthus axinellae*, *Corallium rubrum*, *Caryophyllia inornata*, *Hoplangia durothrix*, *Leptopsammia pruvoti* and *Madracis pharensis*), and (3) the biocoenosis of caves and tunnels in total darkness (*biocénose des grottes et boyaux à obscurité totale* - GO), which is characterized by sponges (e.g. *Petrobiona massiliana*), serpulid polychaetes and motile crustaceans.

Riedl (1966) studied marine caves with different morphologies in the Tyrrhenian Sea (Gulf of Naples) and the Adriatic coasts (Croatia), and suggested a different scheme of biological zonation, based on the distribution of hydroids, macroalgae and the general physiognomy of the assemblages. Specifically, he distinguished 6 biotic zones: (I) *Phytal-Schattengebiet* (shady phytal zone); (II) *Höhlen-Eingangsgebiet* (cave entrance zone); (III) *vordere Bestandsgebiete* (anterior cave zone); (IV) *zentrale Bestandsgebiete* (central cave zone); (V) *hintere Bestandsgebiete* (posterior cave zone); and (VI) *das "leere Viertel"* (the "empty quarter" – a nearly azoic zone). This zonation scheme is typical of blind-ended caves, but may not apply to marine caves with different topography. The boundaries and extent of the different zones depend on the topographic features of each cave (e.g. entrance width to cave length ratio, substrate inclination at the cave entrance, and number of entrances), which affect light gradients and water confinement along the cave. Therefore, even neighbouring marine caves could exhibit biotic heterogeneity due to their different morphology and cave-specific topographic features. For instance, the above zones generally tend to shift outwards with increasing depth while some zones could be absent from tunnels with multiple entrances, which receive more sunlight and are characterized by a higher hydrodynamic regime.

Pouliquen (1972) studied marine caves in Marseille area and concluded that the benthic biocoenoses described from marine caves in previous studies could present differences or be absent from different types of caves. Therefore, he distinguished three types of marine caves according to their bathymetry: (1) superficial caves, partly emerging above the sea level, where no clear patterns of biological zonation occur due to their high hydrodynamic regime; (2) semi-superficial caves, located at a depth of down to 5 m, which are also characterized by high hydrodynamics but exhibit biological zonation shaped mainly by the water flow; and (3) deep caves, which are located at a depth of >10 m and are generally bigger, where light and hydrodynamics decrease inwards and generate a marked biological zonation. While in the first two categories hydrodynamics is the main factor shaping biological zonation, in the deeper caves currents and water renewal greatly depend on the cave morphology and size.

A landmark study on dark submarine caves was published by Harmelin *et al.* (1985), who characterized these unique environments as "extreme habitats"

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[2] Vacelet (1959) reported that at the cave entrance zone a transitional community between the phototophilic algae and the coralligenous biocoenoses can develop (also known as pre-coralligenous). However, according to Laborel (1961) coralligenous concretions are not the most characteristic feature of marine cave communities which are dominated by sessile animals, with *Corallium rubrum* being the most typical species.

[3] Pérès (1967) noticed that the presence of ferromanganese oxides in dark marine caves reminds the formation of nodules in deep oceanic sediments under aphotic conditions. Bianchi *et al.* (1986) and Allouc & Harmelin (2001) studied in detail the structure of this coating in marine caves of North-Western Italy and South France, respectively.

[4] Pérès (1967) highlighted that the coralligenous biocoenosis can develop both outside and inside marine caves, while several species of the semi-dark cave biocoenosis can be found as "enclaves" in dark holes and crevices of coralligenous formations. The presence of extensive coralligenous formations at the entrance zone of submarine caves has been reported from several Mediterranean areas (e.g. Ballesteros, 2006; Kipson *et al.*, 2011; Teixidó *et al.*, 2011b; Gerovasileiou *et al.*, 2017).

and "refuge biotopes". According to this study, the two principal factors affecting the characteristics of the cave communities are the absence of light and the confinement[5], which often act in combination, generating isolation and oligotrophy. The transition from the semi-dark (GSO) to the dark cave biocoenosis (GO) is marked by a remarkable decrease of biotic cover, biomass and species richness (with the exception of serpulid polychaetes), the disappearance of erect growth forms and their replacement by encrusting forms. However, in this transitional zone, encrusting bryozoans (e.g. *Onychocella marioni*) often form nodular bio-constructions on the ceiling of caves, thus creating a vertical zonation. Harmelin *et al.* (1985) also noticed that the dark cave biocoenosis could be further sub-divided in two zones, characterized by different biotic covers (50-80% and 10-40% of the hard substrate, respectively), while in anchialine caves, two additional zones can occur (i.e. the first being inhabited only by small-sized sponge specimens and scattered serpulids, and the terminal zone where sessile fauna disappears).

However, they highlighted that cave topography could greatly affect the above zonation patterns; for instance, biotic cover in tunnels with good water circulation could reach 100% of the hard substrate even in the totally dark zone.

More recently, Bianchi & Morri (1994) studied 17 marine caves in Italy (Ligurian Sea, Tyrrhenian Sea, Sardinia and Sicily Channel) and 4 in the Maldives (Indian Ocean) and distinguished 6 ecological zones, combing the zonation schemes proposed by Riedl (1966) and Harmelin *et al.* (1985) with their findings, and adjusting the scheme of increasing degree of confinement for transitional coastal ecosystems by Guelorget & Perthuisot (1983, 1992). According to this scheme, the different zones are defined as: (1) Zone I, which corresponds to the "periphery" of the marine cave ecosystem, consisting of the external assemblages developing close to the cave entrance; (2) Zone II, which represents the cave entrance and is still bionomically related to the previous zone; (3) Zone III, that is the fore cave, located shortly after the cave entrance, where macroalgae disappear and the benthic communities acquire the typical cave physiognomy; (4) Zone IV, which represents the confined part of the cave, lacking passive filter feeders and dominated by sub-massive sponges; (5) Zone V, encompassing more confined sectors of the cave where biotic cover is much lower than 100% and the community is composed by a thin layer of mostly encrusting organisms (sponges, bryozoans, serpulids, and scleractinians); and (6) Zone VI, which is highly confined and the biotic cover is less than 10%, consisting mainly of serpulids, some scleractinians and very few sponges.

However, most of the above-mentioned bionomic studies provided mainly qualitative (e.g. taxonomic) and semi-quantitative descriptions of the benthic community structure in marine caves, mostly located in the North-Western Mediterranean basin, and rarely quantified spatial variability using biotic surface cover or diversity measures. To date, only a small number of studies have investigated marine cave benthos in a quantitative manner, using either scraped quadrats or photographic non-destructive methods (e.g. Cinelli *et al.*, 1977; Gili *et al.*, 1982; Pansini & Pronzato, 1982; Balduzzi *et al.*, 1985, 1989; Corriero *et al.*, 2000; Martí *et al.*, 2004a,b; Bussotti *et al.*, 2006; Radolović *et al.*, 2015; Gerovasileiou & Voultsiadou, 2016; Gerovasileiou *et al.*, 2017; Sanfilippo *et al.*, 2017; Dimarchopoulou *et al.*, 2018; Rosso *et al.*, 2019). The continuous development of non-destructive photographic methodologies, including photogrammetry, has already assisted in the quantitative study and depiction of marine cave benthos and its distribution (Bianchi *et al.*, 2004; Gerovasileiou *et al.*, 2013; SPA/RAC-UN Environment/MAP & OCEANA, 2017 and references therein).

However, it should be emphasized that almost all the above-mentioned bionomic studies have focused on hard substrate communities and only a few studies have so far investigated sediment macro- and meiobenthos in marine caves of France, Italy and Spain (e.g. Monteiro-Marques, 1981; Bianchi *et al.*, 1986; Akoumianaki & Hughes, 2004; Todaro *et al.*, 2006; Navarro-Barranco *et al.*, 2012; 2013a,b, 2014; Janssen *et al.*, 2013; Romano *et al.*, 2018).

3.3. Environmental gradients and ecosystem functioning

The dramatic environmental gradients in Mediterranean marine caves attracted the interest of several researchers from an early stage. As explained before, the disappearance of light and the effect of water movement inside caves, depending on cave geomorphology (e.g. blind-ended versus tunnels; deeper versus shallower caves), were the first abiotic parameters considered in the bionomic description of different biotic zones and biocoenoses in marine caves (e.g. Pérès & Picard, 1949, 1964; Riedl, 1966; Harmelin, 1969; Cinelli *et al.*, 1977; Harmelin *et al.*, 1985; Balduzzi *et al.*, 1989; Zabala *et al.*, 1989; Bianchi & Morri, 1994). However, only a small number of studies have investigated abiotic parameters (e.g. temperature, salinity, sedimentation rate, pH, oxygen concentration) inside marine caves, aiming at understanding species distribution patterns and ecosystem functioning (e.g. Passelaigue & Bourdillon, 1985; Riera *et al.*, 1985; Gili *et al.*, 1986; Sgorbini *et al.*, 1988; Fichez, 1991a). The detailed study of several environmental parameters in marine caves of Marseille, in France, by Fichez (1989, 1990a,b,c, 1991a,b,c) and in the Grotta Marina of Bergeggi, in Italy (Bianchi *et al.*, 1986; Sgorbini *et al.*, 1988; Morri *et al.*, 1994a) revealed an extreme

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[5] The term "confinement" in relation to water renewal and the replacement of "vital elements" (trace elements, vitamins, etc.) of marine origin was introduced by Guelorget & Perthuisot (1983, 1992) for transitional coastal ecosystems but was later adopted by marine cave researchers (Harmelin *et al.*, 1985; Bianchi & Morri, 1994).

impoverishment of the food intake observed in the more confined cave sectors (trophic depletion hypothesis). This occurs through different mechanisms that determine both the quantitative decrease of the nourishment (e.g. lower absolute quantity, reduction of the flow) and its qualitative degradation (high carbon/nitrogen ratio, greater proportion of complex compounds, decrease in the percentage of sugars, decrease in the ratio between chlorophyll-*a* and phaeopigments, etc.). However, the exploration of marine caves with internal sulphur springs in Capo Palinuro (Italy) shed light on a unique ecosystem which is based on microbial chemo-litho-autotrophy, resembling deep-sea hydrothermal vents (e.g. Abbiati *et al.*, 1992; Cinelli *et al.*, 1994; Bianchi *et al.*, 1994; Southward *et al.*, 1996).

The study of matter and energy flow in Mediterranean marine caves provided a better understanding of their trophic structure and ecosystem functioning, through the development of theoretical models (Ott & Svoboda, 1978; Russo & Bianchi, 2003; Rastorgueff *et al.*, 2015a). Particular animal behaviours, such as the nychthemeral horizontal migrations of swarm-forming mysids and schooling fish, were found to have a pivotal role in mitigating trophic depletion in caves (Riera *et al.*, 1991; Coma *et al.*, 1997; Rastorgueff *et al.*, 2011, 2015a,b; Bussotti *et al.*, 2017, 2018). Nevertheless, there are still important gaps regarding the environmental status and functioning of marine cave ecosystems, since all the above studies have so far focused on a small number of caves from the Western Mediterranean Sea. Such information is crucial in order to monitor dynamics and potential changes of marine cave communities and provide evidence-based conservation.

Slipper lobster *(Scyllarus arctus)* on a dark cave wall.
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Shallow semi-submerged tunnels.
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4. ENVIRONMENTAL & BIOLOGICAL GRADIENTS

A striking characteristic of marine cave communities is that they present a marked zonation due to steep environmental gradients, even within a scale of a few meters. The main drivers generating this zonation are explained below.

4.1. Main environmental gradients

4.1.1. Light availability

The elimination of light obviously plays a pivotal role in shaping community structure and distribution of biota in marine caves, constituting a liming factor for the development of space-competing primary producers, and thus, providing vital space for the development of sciaphilic sessile invertebrates (Pérès & Picard, 1949; Riedl, 1966; Cinelli *et al.*, 1977; Balduzzi *et al.*, 1989; Corriero *et al.*, 2000; Martí *et al.*, 2004a; Gerovasileiou *et al.*, 2017). Light level has been traditionally used for distinguishing the two marine cave biocoenoses, those of semi-dark and dark caves, respectively (Pérès & Picard, 1964). Although threshold values for light intensity in these two cave zones are often arbitrary, it has been suggested that sciaphilic animal-dominated communities develop in cave sectors where light intensity is <1% of the sunlight at the sea surface, while the dark cave biocoenosis develops where light levels are significantly lower than 0.01% of the sea surface levels, respectively (Harmelin *et al.*, 1985; Bianchi *et al.*, 1986). According to Passelaigue (1989), the decrease in light intensity in shallow marine caves is similar to that occurring from 50 to 400 m depth in the open sea. As expected, light intensity decreases with depth (e.g. shallow vs. deeper caves) and is affected by cave-specific topographic features, such as entrance width to cave length ratio, substrate inclination and orientation, number of entrances and secondary openings (Riedl, 1966). Thus, entrance zones in shallow semi-submerged caves and tunnels with multiple openings receive more sunlight compared to submerged blind-ended caves, and within caves, ceilings and overhangs tend to be darker compared to vertical walls, even when they are located at the same distance from the entrance (Riedl, 1966, Pouliquen, 1972; Bianchi & Morri, 1994; Martí *et al.*, 2004a; Gerovasileiou *et al.*, 2017).

4.1.2. Water circulation and associated parameters

The study of tunnel-shaped caves, however, showed that the absence of light is not the only driver for the development of the dark cave biocoenosis, since biotic cover may be remarkably high throughout the length of the cave, even reaching 100% of the hard substrate in dark zones (Riedl, 1966; Harmelin, 1969; Harmelin *et al.*, 1985). Therefore, it was intuitively accepted that water circulation constitutes an important key factor for determining the structure and type of benthic communities in marine caves (Riedl, 1966; Harmelin *et al.*, 1985; Gili *et al.*, 1986; Balduzzi *et al.*, 1989; Zabala *et al.*, 1989).

According to Fichez (1991c), water residence time in marine caves ranges from one day at the entrance zone to over eight days in the inner confined sectors. Based on current measurements and an accurate topographic data which allowed reconstructing the cave geometry, Bianchi *et al.* (1998) calculated the water balance of the Grotta Azzurra (Tyrrhenian Sea, Italy). In the tunnel-shaped sectors of the cave, water exchange was caused by the flow between the two opposite entrances. With a slightly rough sea, water was completely renewed in less than half an hour, while during calm weather conditions, the complete replacement took a few hours. In the blind end of the cave (known as "Sala della Neve" = Snow Hall), water was exchanged only by diffusion. A particle of water that travels along the entire perimeter of the chamber would take more than two and a half hours under calm seas, but only a quarter of an hour in the presence of a current speed of 10 cm·s^{-1}. Should we accept that the water turnover rate is an adequate estimate of confinement, these calculations indicate that not even the blind-ended part of the Grotta Azzurra is confined. This result suggests that confinement does not depend only on the shape of the cavity (blind-ended or tunnel-shaped) but also on its size: large caves with wide chambers are less affected by confinement, as the presence of large masses of water probably allows the onset of density gradients and internal currents.

The study of Grotta Marina of Bergeggi (Ligurian Sea, Italy) by Morri *et al.* (1994a) showed that water movement affects a series of hydrological parameters which define the quality of seawater, such as temperature, salinity, oxygen concentration, pH and sedimentation rate. The role of these parameters has been investigated in several publications (e.g. Passelaigue & Bourdillon, 1985; Riera *et al.*, 1985; Gili *et al.*, 1986; Sgorbini *et al.*, 1988; Fichez, 1991a). For example, Gili *et al.* (1986) studied a submerged cave in Medes Islands (Catalonia, Spain) and showed that salinity, temperature, density, dissolved oxygen, chlorophyll-*a* and pigments inside did not differ significantly from those outside the cave due to the constant water exchange.

Water circulation also affects biotic parameters such as the removal of catabolites, larval dispersal and food supply (Balduzzi *et al.*, 1989). It has been calculated that there is a close relationship between the cave volume and available nutritional reserves: in the absence of water renewal, a cave of 10 m^3 has reserves for an hour and a cave of 1 m^3 for only 8 minutes (Riedl, 1966). Thus, due to the absence of autochthonous primary production, cave communities greatly depend on external food supply. Since benthic communities in caves are dominated by filter feeders, this food will essentially be represented by the organic substance that is suspended in the water. Confined environments,

therefore, will have a significantly lower food intake; this is known as the trophic depletion hypothesis (Zabala *et al.*, 1989; Fichez, 1990b; Bianchi & Morri, 1994). This hypothesis was confirmed in a marine cave near Marseille (Fichez, 1989, 1990a,b,c, 1991a,b,c) and partly in Grotta Marina of Bergeggi (Bianchi *et al.*, 1986; Morri *et al.*, 1994a). The extreme impoverishment of the dietary intake observed in the confined cave zones occurs through different mechanisms determining both the quantitative decrease of the nourishment (e.g. lower absolute quantity, reduction of the flow) and its qualitative degradation (e.g. high carbon to nitrogen ratio, greater proportion of "complex" compounds, decrease in the percentage of sugars, decrease in the ratio between chlorophyll and phaeopigments).

4.1.3. Current speed

Pansini & Pronzato (1982) and Balduzzi *et al.* (1989) estimated water movement in the Grotta della Cala di Mitigliano (Tyrrhenian Sea, Italy), using plaster balls, whose consumption is proportional to the agitation of the water. Using this same method, and applying the empirical formula $v = 3.65 \times (M/B-1)$ (where v is the velocity in $cm \cdot s^{-1}$, M is the % weight loss of the balls after 24 h, B is the % weight loss of the reference balls, placed in still water), Sgorbini *et al.* (1988) calculated the current speed in the Grotta Marina of Bergeggi. Due to the general tunnel conformation of this cave, water movement was relatively homogeneous throughout the cave, with current speed being 12-20 $cm \cdot s^{-1}$, except for internal "lakes" and lateral chambers where water flow was significantly slower. In the same cave, Morri *et al.* (1994a) found a significant positive correlation between the values of current speed and the amount of biological cover observed on the cave walls. Bianchi *et al.* (1998) measured the current speed in the Grotta Azzurra (Tyrrhenian Sea, Italy) using magnetic induction current metres and found that during calm sea conditions current speed inside the cave was lower than 2 $cm \cdot s^{-1}$. During slightly rough sea conditions current speed inside the cave was 6-10 $cm \cdot s^{-1}$, while more intense currents are expected with rough seas.

Current speed within caves can affect the structure of benthic communities. A number of studies have suggested that the decrease of sponge morphological diversity (i.e. dominance of encrusting growth forms) and species number/diversity in the intermediate corridors of marine caves are related to the locally stronger flow rates due to the Venturi effect (i.e. velocity of the fluid increases as the cross-sectional area decreases), which is caused by the cave narrowing (Pansini *et al.*, 1977; Bell, 2002; Gerovasileiou & Voultsiadou, 2016).

4.1.4. Water temperature

Water temperature inside marine caves depends on several parameters, such as local environmental conditions, water circulation, exposure to the open sea, cave morphology and bathymetry, presence of internal springs and freshwater infiltrations, etc. Water temperature difference between the inner sectors of marine caves of Marseille region (France) and the external environment could reach up to 7°C, with the entrance zone being more severely affected by temperature fluctuations (Pouliquen, 1972; Harmelin *et al.*, 1985; Passelaigue & Bourdillon, 1985). In the Grotta Marina of Bergeggi (Italy) the innermost portions of the cave exhibited less variable temperatures all year round with respect to the entrance zone (Bianchi *et al.*, 1986). Martí *et al.* (2004a) studied a semi-submerged cave in Cabrera Island (Balearic Islands, Spain) and a submerged cave in Medes Islands (Catalonia, Spain) and found no differences in water temperature between different cave zones or seasons (June and November) within each cave (the average temperature was 19°C in the Cabrera cave and 17°C in the Medes cave). On the other hand, Radolović *et al.* (2015) measured water temperature in the shallow horizontal Y-Cave (Dugi Otok Island, Croatia), using data loggers year-round (August 2003 to July 2004) and found a notable water stratification despite the fact that the cave is shallow and exposed to the open sea. More specifically, they found: (a) retention of a colder water layer along the bottom of the cave interior during summer, attributed to the cave morphology; (b) retention of cold brackish water (18-22°C) on the sea surface in an intermediate semi-submerged chamber during summer; and (c) retention of warmer water (>15°C) in upper parts of the cave during winter, possibly due to the mixing of freshwater and seawater.

One of the most characteristic examples on the role of cave morphology in water stratification inside caves is that of 3PP Cave in Marseille (France). The cave presents an inwardly descending profile which, in combination with the presence of a berm at the entrance (3 m above the ceiling and 10 m above the bottom of the internal chamber), is responsible for a rare pattern of hydrological stratification: the inner cave chamber is filled with cold, density-trapped seawater which remains nearly homeothermic all year round (12.8 to 14.5°C) compared to external water at the same depth (13.0-24.7°C in 1991) (Vacelet *et al.*, 1994, Harmelin, 1997). These conditions, combined with the darkness and oligotrophy in the inner cave, allow for the colonization of deep-sea species, such as the hexactinellid sponge *Oopsacas minuta*, whose propagules are upwelled from the nearby Cassidaigne Canyon (Vacelet *et al.*, 1994; Harmelin & Vacelet, 1997).

According to Chevaldonné & Lejeusne (2003) the maximum water temperatures recorded from caves of Marseille area, which have an ascending profile, reach up to 24°C, usually for relatively short periods. For example, while temperature inside the descending 3PP Cave remains low year-round, temperature fluctuations inside Jarre Cave follow those of the external environment, occasionally rising up to 24°C (2001-2002 data). In the Eastern Mediterranean Sea, water temperature in shallow semi-submerged caves of the Aegean Sea (Greece) can reach up to 26-28°C during summer, while it is lower (18-23°C) in deeper, entirely submerged caves (2010-2018 unpublished data by

V. Gerovasileiou). In shallow caves of Lebanon which receive freshwater input, temperature in the seawater layer was reported to reach 27-28°C while in the freshwater layer it was 21°C (September 2002 and July 2003, data in Pérez et al., 2004).

4.1.5. Freshwater input
In several cases, freshwater infiltrations (usually sporadic or seasonal) at the inner and upper sectors of marine caves (e.g. cave ceilings at inner chambers with an ascending profile) are responsible for the local impoverishment or even disappearance of sessile benthos and the creation of azoic zones (Riedl, 1966; Pouliquen, 1972; Balduzzi et al., 1985; Harmelin et al., 1985; Radolović et al., 2015). Harmelin et al. (2003) reported that salinity at the bell-shaped ceiling of the inner chamber of Bagaud Cave (Port-Cros, France) ranged from 5.3 to 22.85 (in March and September, respectively) while its values at the entrance and outer chamber were 38.1-38.4. The occurrence of some rare sessile taxa and/or bio-constructions only in a small number of caves with freshwater input is possibly related either to salinity gradients or the provision of organic material and nutrients. Such cases include the rare scleractinian *Guynia annulata* in marine caves of Marseille and Crete (Zibrowius, 1978), the development of particular types of "biostalactites" by the serpulid *Protula tubularia* in caves of Otranto Cape, Sicily, Lesvos Island and Crete (Belmonte et al., 2009; Guido et al., 2014; Sanfilippo et al., 2015, 2017; Gerovasileiou, unpublished data), and lithistid (rock) sponges which are probably favoured by the rich silicate content of freshwater input in marine caves of Lebanon and Crete (Pérez et al., 2004; Pisera & Gerovasileiou, 2018).

4.1.6. Sedimentation
Cave walls in highly confined chambers with a low hydrodynamic regime, walls with positive inclination in proximity to the muddy bottom, protuberances and cavities on vertical walls and rocky boulders on the cave floor are often covered with a thin layer of sediment. These surfaces are usually colonised only by a small number of sessile taxa which can tolerate high sedimentation levels (Laborel & Vacelet, 1958; Pouliquen, 1972; Zabala & Gili, 1985; Gerovasileiou & Voultsiadou, 2016; Gerovasileiou et al., 2017; Dimarchopoulou et al., 2018; Sempere-Valverde et al., 2019). For instance, erect growth forms (e.g. sponges *Axinella* spp.), which often develop on walls covered by a sediment layer, can better cope with high sedimentation rates since their body shape helps to avoid clogging of their aquiferous system (Bibiloni et al., 1989; Gerovasileiou & Voultsiadou, 2016).

4.2. Biological gradients

As a response to the steep environmental gradients, almost all structural parameters used to describe the organization of biological communities also exhibit gradients from the entrance to the interior of the caves (Harmelin et al., 1985; Balduzzi et al., 1989;

Martí et al., 2004a; Gerovasileiou & Voultsiadou, 2016; Gerovasileiou et al., 2017).

4.2.1. Biological cover and abundance
One of the most widely used parameters for the quantification of benthic community patterns on hard substrates is the biotic cover, i.e. the percentage of substrate they occupy, as a measure of organismal abundance. From values around 100%, typical of the external environment, biotic cover progressively decreases and can even reach zero in the terminal sectors of blind-ended caves, where the sessile fauna is almost absent, except for some serpulids (Riedl, 1966; Harmelin et al., 1985; Balduzzi et al., 1989; Bianchi & Morri, 1994; Gerovasileiou et al., 2017). Based on biotic cover, Harmelin et al. (1985) distinguished two zones within the dark cave biocoenosis: zone 1, with a cover of 50-80%; and zone 2, with a cover of 10-40%, respectively. In blind-ended caves, the decrease of cover appears to be related to the decrease of light from the semi-dark to the dark cave sector, and to the reduction of water movement within the inner dark sector. On the other hand, in tunnel-shaped caves with constant water renewal biotic cover could reach 100% of the hard substrate even in the totally dark zone (Harmelin, 1969; Harmelin et al., 1985). Therefore, cave topography greatly affects zonation patterns of biotic cover (Balduzzi et al., 1989; Morri et al., 1994a; Gerovasileiou et al., 2017; Dimarchopoulou et al., 2018).

The only existing study on hard substrate meiofauna has shown that while abundance increased from the entrance to the middle part of the studied cave (Grotta di Ciolo, Salento, Italy), there was a small increase towards the inner dark zone of the cave (Russo et al., 2015). Regarding macro- and meiofauna in sediments of the cave floor, the few existing studies have shown contrasting results, and thus, spatial patterns of abundance cannot be generalised (see sub-section 5.4).

4.2.2. Diversity
Species number and Shannon-Wiener (H′) diversity decrease inwards, especially in blind-ended caves, in a similar way to biotic cover (Pansini et al., 1977; Balduzzi et al., 1989), although the trends are often irregular due to patchiness of benthos (Harmelin, 1985; Harmelin et al., 1985). For example, Balduzzi et al. (1989) observed a gradual decrease in the number of species in the Grotta della Cala di Mitigliano, a blind-ended cave over 80 m long, with sessile species shifting from 60 to 10.

However, in several caves, the above diversity measures were found to increase from the well-lit entrance to the semi-dark sectors, and then decreased inwards (Sarà, 1962b; Cinelli et al., 1977; Corriero et al., 1997a, 2000; Bell, 2002; Gerovasileiou & Voultsiadou, 2016; Dimarchopoulou et al., 2018), or they even kept increasing to the innermost cave sectors (Martí et al., 2004a,b), which are characterized by diverse animal-dominated communities. Such divergent patterns are generally attributed to cave-specific topographic features which generate gradients of

abiotic and biotic features. Of course, these trends vary with taxon, different animal groups dominating in different cave sectors (see chapter 5).

According to the biodiversity census for Mediterranean marine caves by Gerovasileiou & Voultsiadou (2014), the highest number of taxa (both sessile and motile) in the existing literature has been reported from the semi-dark cave zone (1120), followed by the cave entrance (985) and the dark zone (844). Nevertheless, for 510 taxa, cave zone was not specified in the sources. Macroalgae dominated in terms of species number in cave entrances (23% of the total diversity) and sponges dominated in the semi-dark and dark zones (19% and 22.4%, respectively).

Regarding macroinfauna and meiofauna, similarly to abundance, the few existing studies have shown contrasting results, and thus, spatial patterns of diversity cannot be generalised (see sub-section 5.4). Macroinvertebrate assemblages associated to sponges and hydrozoans in marine caves of the Aegean (Gerovasileiou et al., 2016a) and Alboran seas (Navarro-Barranco et al., 2014), respectively, were found to exhibit an inwards decrease in species richness.

4.2.3. Biomass

Although biomass measurements (i.e. the quantity by weight of living matter per unit area) have rarely taken place in marine caves, a sharp decrease from the entrance towards the cave interior has been evidenced, similarly to biotic cover and diversity (True, 1970; Fichez, 1989, 1990b; Gili et al., 1986; Zabala et al., 1989). Gili et al. (1986) studied a blind-ended cave in Medes Islands (Catalonia, Spain) and found that biomass, expressed in ash-free dry weight m^{-2}, decreased from the entrance (0.26 kg·m^{-2}) to the inner end (0.08 kg·m^{-2}). Measurements carried out in the Grotte des Trémies (Marseille, France) by Fichez (1989), showed that from the semi-dark to the dark cave zones, biomass is reduced to less than 10%. Specifically, the infaunal biomass shifts from 3.4 ± 0.4 g·m^{-2} to 0.3 ± 0.2 g·m^{-2}, while the epifaunal biomass shifts from 305.1 ± 33.6 g·m^{-2} to 29.7 ± 22.0 g·m^{-2}.

4.2.4. Volumetric stratification

Increasing confinement and subsequent oligotrophy towards the innermost dark cave sectors causes a reduction in size and a selection of morphological groups, with the progressive replacement of erect growth forms by encrusting ones inwards (Harmelin et al., 1985; Bianchi & Morri, 1994; Rastorgueff et al., 2015a; Gerovasileiou & Voultsiadou, 2016; Gerovasileiou et al., 2017). In marine caves of the North-Western Mediterranean basin, sessile benthic communities at the entrance and outer cave zones are typically characterized by a well-developed upper layer that is higher than a decimetre, with gorgonian species (e.g. *Eunicella cavolini* and *Paramuricea clavata*) protruding into the water column even for more than half a meter (Harmelin et al., 1985; Morri & Bianchi,

2003). In semi-dark cave sectors, the height of the upper layer drops to a few centimetres, reaching a maximum of 10-20 cm in the case of well-developed populations of red coral (*Corallium rubrum*). In the inner cave sectors, benthic community may appear monolayered, even in the case of a 100% substrate cover, but in the transitional zone to the dark zone, it may have a thickness of a few centimetres due to the formation of bryozoan nodules (Harmelin et al., 1985; Harmelin, 2000; Rosso et al., 2019). Finally, in a dark cave, sessile communities are mostly encrusting, and the upper layer usually does not exceed 1 cm in height (e.g. serpulid tubes whose terminal edge arises from the substrate to the water column in order to escape the boundary layer stagnation) (Morri & Bianchi, 2003). In the Eastern Mediterranean basin, where large cnidarians are typically absent from the outer cave zones, the upper biotic layer may be formed by massive/tubular and arborescent sponges (Gerovasileiou et al., 2017).

4.3. A biological scale of hydrological confinement

Biological gradients in marine caves largely depend on the degree of hydrological confinement (i.e. a hydrodynamic concept related to water exchange) in relation to water renewal and the replacement of "vital elements" (trace elements, vitamins, etc.) of marine origin (Harmelin, 1980; Harmelin et al., 1985; Bianchi & Morri, 1994). In marine ecology, the notion of confinement has known a much broader resonance among scholars studying transitional coastal (e.g. paralic/lagoonal) ecosystems (Guelorget & Perthuisot, 1983, 1992), but has been also introduced and applied in marine cave ecology. As pointed out by Guelorget & Perthuisot (1983, 1992), confinement is a complex and abstract concept, which cannot be accurately expressed quantitatively without a unit of measurement. Nevertheless, the same authors stress that confinement ultimately expresses a concept of hydrodynamic nature, and thus, it depends primarily on current velocity and water turnover.

Similarly to transitional coastal ecosystems, a confinement scale has been defined for marine caves, taking into consideration three main parameters: (1) the composition, with reference to the trophic groups and the dominant growth forms; (2) spatial organization, and above all the presence of an upper layer; (3) the total biotic cover of the substrate. Bianchi & Morri (1994) carried out a first test of the biological confinement scale in the Grotte del Bue Marino in the Island of Gorgona (Livorno, Italy), two parallel caves with a predominantly sub-horizontal development. The morphological characteristics of these caves, and specifically the fact that they both have a simple linear development and blind-ended shape, can be considered "paradigmatic conditions" of hydrological confinement. In addition, the fact that these are two adjacent "twin" cavities appeared advantageous to compare directly

the observed biological zonation. In both cavities a marked gradient of reduction of biological cover from the outside to the inside was observed. Six bionomic zones were identified on a physiognomic basis, indicated with Roman numerals (Fig. 4.1):
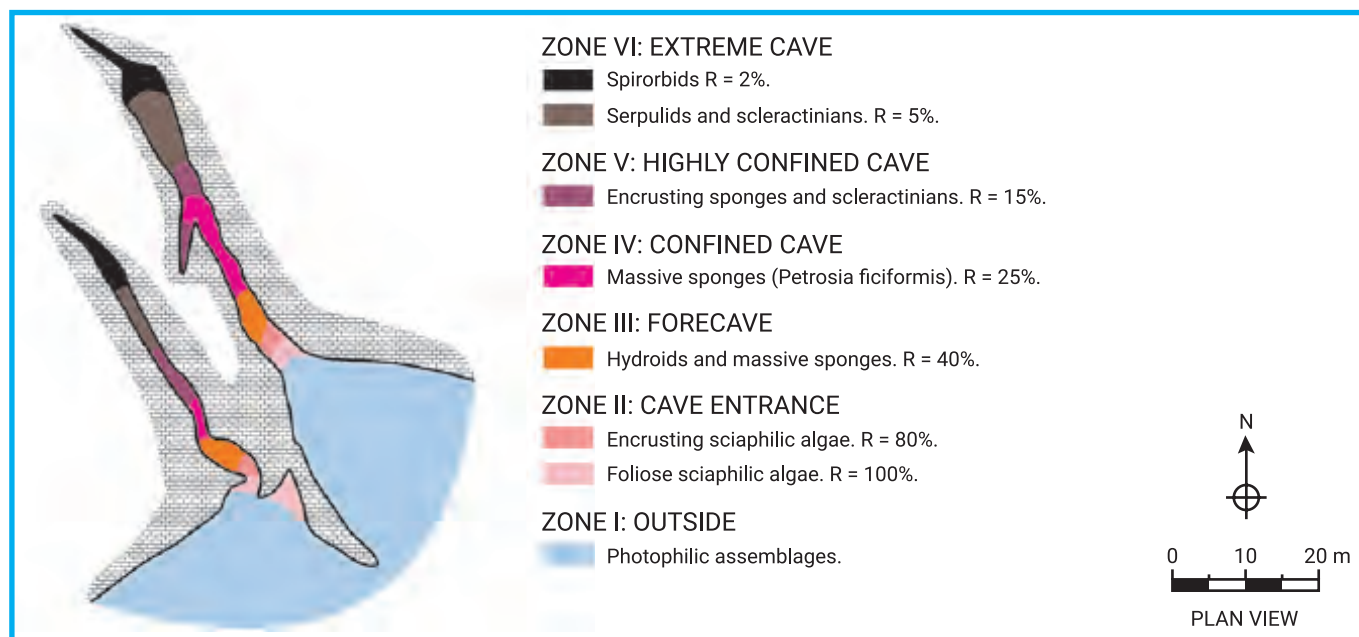
Fig. 4.1. Main biological assemblages in the Grotte del Bue Marino (Gorgona Island, Italy) and their zonation according to the confinement gradient. R: biological percent cover of the substrate. From Bianchi & Morri (1994).

- **Zone I** corresponds to the "periphery" of the marine cave ecosystem, consisting of the external assemblages developing close to the cave entrance. The community is multi-layered, with the presence of an upper layer and high biological cover.

- **Zone II** is located at the entrance of the cavity. The community structure here is less complex than that of the previous zone, to which it remains bionomically related, but the cover is still high. In some cases, it can be considered an enclave of deeper sciaphilic biocoenoses.

- **In zone III**, shortly after the entrance, macroalgae disappear and the assemblages acquire the typical "cave physiognomy", appearing significantly different to those of the external in terms of composition and spatial organization. However, the water turnover is still high, and thus, the effects of confinement are not recognizable. The most characteristic elements of this zone are the erect passive filter feeders (e.g. hydroids and octocorals) which dominate or overlap an assemblage consisting mostly of massive forms, with sponges, ascidians and bivalves. The cover can decrease to around 40% of the hard substrate.

- **Zone IV** represents the confined part of the cave where cover typically decreases. Passive filter feeders are absent and thus, the upper layer is completely missing. The substrate is occupied mainly by massive or sub-massive sponges.

- **Zone V** encompasses more confined sectors of the cave where the biotic cover is much lower than 100%

and the benthic community is composed of a single thin layer of mostly encrusting organisms (sponges, bryozoans, serpulids, and scleractinians).

- **Zone VI** is highly confined and the biotic cover is less than 10% and can be further reduced in the terminal portions of the cave, consisting mainly of serpulids, some scleractinians and very few sponges.

Thanks to the study of numerous caves, different in size, depth and topography, in several sectors of the Mediterranean (Ligurian Sea, Tyrrhenian Sea, Sardinia and Sicily Channel) and a comparison with some extra-Mediterranean caves (Maldives, Indian Ocean), Bianchi & Morri (1994) developed a scale of confinement comprising 6 degrees:

- **Degree 0 -** The external environment, located upstream of zone I.

- **Degree 1 -** The cave entrance, which is a transitional area between zones I and II, marked by the simplification of the assemblage structure, especially by the reduction of the upper layer.

- **Degree 2 -** Radical modification of the assemblage (disappearance of macroalgae), which begins to exhibit a typical cave physiognomy (between zones II and III).

- **Degree 3 -** Disappearance or severe decrease of passive filter feeders, especially the erect ones (between zones III and IV).

- **Degree 4 -** Disappearance or severe decrease of massive forms (between zones IV and V).

- **Degree 5 -** Disappearance of encrusting forms (between zones V and VI).

- **Degree 6 -** Disappearance of the sessile fauna. Marginal (Riedl & Ozretic, 1969) and anchialine caves (Stock *et al.*, 1986), which lack direct connection with the sea, are characterized by highly confined conditions, beyond the sixth degree of confinement of the above scale.

Leopard-spotted goby *(Thorogobius ephippiatus)* and mysids on a muddy cave bed.
© V. Gerovasileiou

Semi-dark cave assemblage with red coral facies (*Corallium rubrum*), scleractinian corals and sponges (e.g. *Petrosia ficiformis*).
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5. BIONOMY

5.1. Bionomic framing and heterogeneity

Within marine caves the environmental gradients are dramatic (Morri *et al.*, 1994a): within a few meters there are variations of light, water movement and trophic input, which, in the external environment, can take place within tens or even hundreds of meters (Sarà, 1978; Bianchi, 1994). As explained in the previous chapter, these environmental gradients generate a marked zonation of cave communities, and thus species are not distributed homogeneously inside caves, but generally prefer distinct sectors (Bianchi *et al.*, 1996; Bianchi & Morri, 1999).

Austrian and French scientists are among the first who committed themselves to defining the typology and distribution of the biological zones inside Mediterranean marine caves (see chapter 3), and thus two models of biological zonation have been suggested (Riedl, 1959b; Pérès & Picard, 1964). However, it should be emphasized that the definition of biological zones in marine caves is based mainly on hard substrate communities. Infaunal communities living in the sediments that sometimes cover the cave floor are generally poor and have not been thoroughly studied (Monteiro-Marques, 1981).

In addition to the general patterns and trends regarding ecological zonation, small-scale variability can be so high, that in some cases heterogeneity between opposite walls or nearby sites within a cave can be higher than between nearby caves with similar morphology (Bussotti *et al.*, 2006; Gerovasileiou & Voultsiadou, 2016). This idiosyncratic behaviour, also known as "individuality", has been attributed to the cave-specific (micro-)topography and the associated environmental gradients and modifications in trophic or larval supply (Riedl, 1966; Balduzzi *et al.*, 1989; Benedetti-Cecchi *et al.*, 1997; Martí *et al.*, 2004a; Bussotti *et al.*, 2006; Gerovasileiou *et al.*, 2013, 2017; Sempere-Valverde *et al.*, 2019). The presence of micro-habitats and unique features (e.g. sulphur springs, freshwater springs, bioconstructions, and secondary openings) within caves could further increase heterogeneity, as they often support distinct communities and rare species (Bussotti *et al.*, 2006; SPA/RAC-UN Environment/MAP & OCEANA, 2017).

Since the first ecological and bionomic studies in Mediterranean marine caves took place mostly in the North-Western Mediterranean (see chapter 3), the first bionomic descriptions by pioneer researchers largely reflected regional conditions and knowledge. The gradual exploration of marine caves towards insular, southern and eastern sectors of the Mediterranean basin, allowed for comparisons, revealing a non-negligible biogeographic heterogene-ity, with several taxa having a restricted distribution range or being common in some areas but absent from others (Gerovasileiou & Voultsiadou, 2012; Bussotti *et al.*, 2015; Gerovasileiou *et al.*, 2015a).

5.2. The biotic zones of Riedl

Riedl (1959b, 1966) studied marine caves with different morphologies in the Tyrrhenian Sea (Gulf of Naples) and the Adriatic coasts (Croatia), and suggested a scheme of biological zonation, based on the distribution of hydroids, macroalgae and the general physiognomy of the assemblages. Specifically, he distinguished the 6 following biotic zones (Fig. 5.1): (I) *Phytal-Schattengebiet* (shady phytal zone); (II) *Höhlen-Eingangsgebiet* (cave entrance zone); (III) *vordere Bestandsgebiete* (anterior cave zone); (IV) *zentrale Bestandsgebiete* (central cave zone); (V) *hintere Bestandsgebiete* (posterior cave zone); and (VI) *das "leere Viertel"* (the "empty quarter" – a nearly azoic zone).

In the phytal zone, the abundance of algae decreases in parallel with the decrease of light, while the sessile fauna dominates towards the interior. The zonation of the different faunal groups depends primarily on the gradients of light and water movement in the entrance area and in the anterior cave zone. For the majority of groups, the abundance is higher in the central cave zone, but is also greatly influenced by the inclination of the substrate. In the posterior zone, under complete darkness and calm waters, the inclination of the substrate (and hence the sedimentation) constitutes an important factor. Finally, the "empty quarter", is characterized by the almost total absence of fauna, the bare rock and the great distance from the entrance: its existence is determined by the scarcity of food supplies, the deterioration of water quality, and by possible freshwater infiltrations.

Comparing different marine caves, three main aspects were considered important in determining the zonation of the biotic zones: the depth, size and shape of the cave. As for the depth, deep-water caves exhibit a marked decrease in flora and fauna, concentration of the fauna near the entrance, while the "empty quarter" is more extensive than in shallow caves. It is also possible to observe the reduction of the phytal assemblage and changes in the composition of the inner assemblages. As for the size of the cave, the "empty quarter" is larger in large caves, while it is smaller or absent in smaller caves.

However, according to Riedl, the most important factor for the distribution of the biota is the shape of the caves. The boundaries and extent of the different zones depend on the topographic features of each

cave (e.g. entrance width to cave length ratio, substrate inclination at the cave entrance, and number of entrances), which affect light gradients and water confinement along the cave. The above zonation scheme is typical of blind-ended caves, but may not apply to caves with different morphology. For instance, the above zones generally tend to shift outwards with increasing depth (Fig. 5.1). In tunnel-shaped caves, where there is constant water movement, but light can be very variable, it is difficult to identify a clear zonation pattern and some zones can be absent.
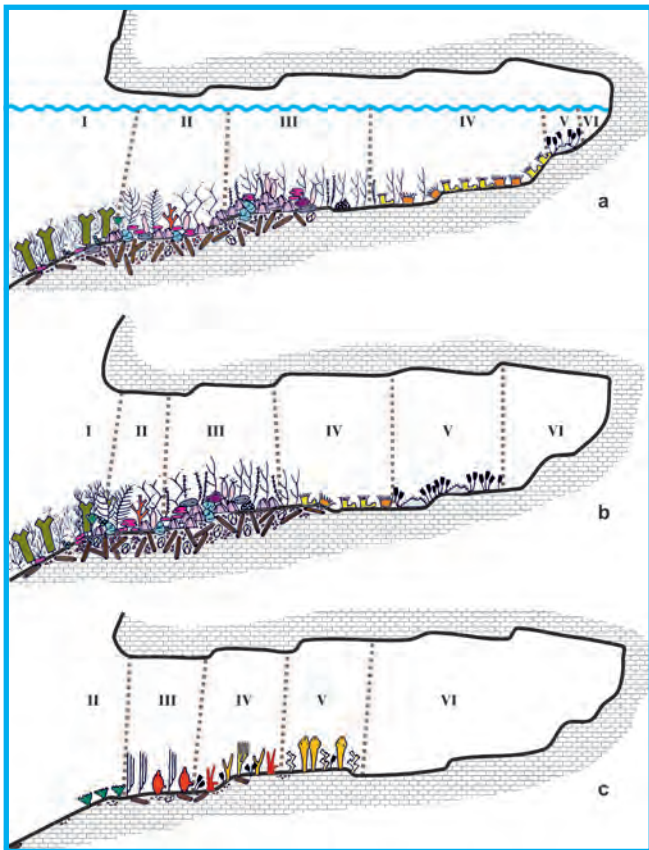

Fig. 5.1. Biotic zones in semi-submerged caves (a), in infralittoral (b) and circalittoral (c) submerged caves according to Riedl (1966). The inner zones can occur close to the cave entrance as the depth increases.
I: algal dominated zone, II: entrance zone, III: anterior zone, IV: central zone, V: posterior zone, and VI: 'empty quarter'.
Redrawn and modified from Riedl (1966).

Riedl noticed that benthic assemblages similar to those of caves can also be found outside, under roofs and overhangs, indicating the pivotal role of the light factor. The exposure to light of a marine cave is affected by five factors: (1) surface illumination; (2) depth; (3) orientation with respect to the cardinal points; (4) the angle of the entrance; and (5) the inclination. Light acts on the cave assemblages both directly and indirectly, favouring the growth of algae. According to Riedl (1966),

the limit for algal development is around 0.5-1% of the surface illumination. Observations and measurements made by Southward *et al.* (1996) at the entrance of the Grotta Azzurra of Capo Palinuro, indicate that with light equal to 17% of that of the surface, the assemblages are still dominated by photophilic algae, in particular by Phaephyceae (*Dictyota*); at 3%, the assemblage becomes sciaphilic, dominated by Rhodophyta (*Peyssonnelia* and encrusting coralline algae), while below 0.8% the assemblage exclusively consists of sessile animals, with sponges, hydroids, scleractinians, bryozoans and colonial ascidians.

The intensity of water movement at a specific point in a cave depends on four factors: (1) the exposure and the profile of the coast; (2) depth; (3) the form and (4) nature of the substrate. The development of cave assemblages requires a water agitation of no more than 2-10% of that of the surface. The biotic zones may be more or less extensive near the entrance to the cave depending on the depth and shape of the cavity. The shape, in particular, can accelerate (narrows) or slow down (widenings) the motion of water, which is reflected on the distribution of indicator species (e.g. hydroids) or from the forms of erosion. The nature of the substrate can also play an important role in the inner parts of the cave.

5.3. The semi-dark and dark cave biocoenoses of Pérès and Picard

In the highly influential "Nouveau manuel de bionomie benthique", which summarized and updated the existing knowledge on Mediterranean benthic communities, Pérès & Picard (1964) distinguished three main biocoenoses develop-ing along the horizontal cave axis (Fig. 5.2): the coralligenous biocoenosis (*biocénose coralligène* - C), which can often develop at the cave entrance[6]; the semi-dark cave biocoenosis (*biocénose des grottes semi-obscures* - GSO), which develops in the semi-dark part of caves and is characterised by a luxuriant and colourful animal growth (mainly sessile filter-feeding invertebrates, e.g. sponges and anthozoans)[7]; the biocoenosis of caves and gulleys in total darkness (*biocénose des grottes et boyaux à obscurité totale* - GO), which is found in completely dark caves and is characterised by a scanty sessile biota (e.g. serpulids) on nearly bare rock, as well as motile fish and crustaceans. The above framework is the most widely followed and accepted to date. An updated description of the semi-dark and dark cave biocoenoses, based on current data from different Mediterranean areas, is presented below.

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[6] For a thorough review on the Mediterranean coralligenous biocoenosis see Ballesteros (2006).
[7] A transitional assemblage between the semi-dark and dark cave biocoenoses can be recognised in some caves.
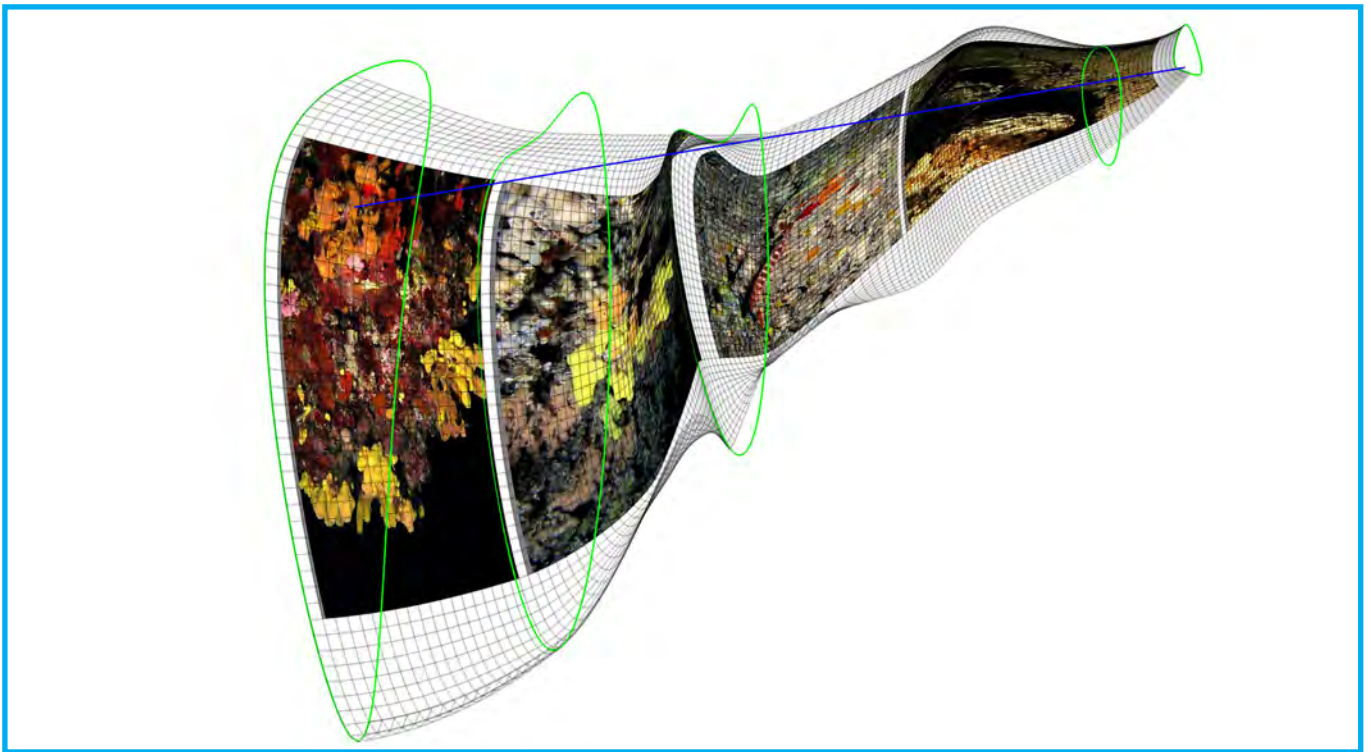
Fig. 5.2. Ecological zonation in a blind-ended cave (24-40 m depth, Agios Vasilios Cave, Lesvos Island, Greece), depicted on a three-dimensional model. Representative images of different communities are superimposed on the cave model. From left to right, the coralligenous biocoenosis of the cave entrance is gradually replaced by the intermediate, animal-dominated semi-dark and the inner dark cave biocoenoses, respectively. Biotic cover decreases and erect growth forms (e.g. sponges, bryozoans and corals) are replaced by encrusting sponges and serpulids. Green circles represent cross-sections of the cave, providing a three-dimensional perspective to the model. The blue line represents the start-to-end cave axis (22 m long). Visualization was made with "cavetopo" software (Gerovasileiou *et al.*, 2013). For detailed descriptions of sessile benthic communities in this cave see Gerovasileiou & Voultsiadou (2016), Gerovasileiou *et al.* (2017), Sanfilippo *et al.* (2017), and Rosso *et al.* (2019).

5.3.1. The semi-dark cave biocoenosis

It is typically found at (or in proximity to) the entrance of caves and even under caverns and overhangs which, topographically speaking, would not be characterised as true caves. The distinction of the GSO biocoenosis from that of the coralligenous, to which it was once assimilated (see chapter 3), is due to Laborel (1960, 1961), who first pointed out its originality. The distinctive feature of this biocoenosis is the fact that it is dominated by sessile animals (e.g. sponges, anthozoans and bryozoans), although some sciaphilic macroalgae (e.g. the chlorophyte *Palmophyllum crassum* and certain encrusting rhodophytes) may occasionally occur in certain caves.

The most frequently recorded sponge species[8] in the semi-dark cave biocoenosis are *Agelas oroides*, *Petrosia ficiformis*, *Spirastrella cunctatrix*, *Chondrosia reniformis*, and *Phorbas tenacior*. Some sponges (e.g. *P. ficiformis* and *C. reniformis*) can be often discoloured due to effect of light decrease on their associated cyanobacteria. The sponge *Aplysina cavernicola* has been also described as a typical species of this biocoenosis in the North-Western Mediterranean basin (Vacelet, 1959). Sponges of the class Homoscleromorpha (e.g. *Oscarella* spp. and *Plakina* spp.) can also have considerable cover in some caves (Gerovasileiou & Voultsiadou, 2016; Grenier *et al.*, 2018).

Three anthozoan facies have been recorded in the semi-dark cave biocoenosis (mostly on ceilings and overhangs) (Pérès, 1967; Zibrowius, 1978): (i) facies of scleractinians, such as *Leptopsammia pruvoti*, *Madracis pharensis* (very abundant in the Eastern Mediterranean), *Hoplangia durotrix*, *Polycyathus muellerae*, *Caryophyllia inornata* and *Astroides calycularis* (mostly in southern areas of the Western Mediterranean); (ii) facies of the red coral *Corallium rubrum* which is more common in the North-Western Mediterranean Sea but can be found in deeper waters (below 50 m) in the North-Eastern basin; and (iii) facies of *Parazoanthus axinellae*, which can be common close to the entrance or in semi-dark tunnels with high hydrodynamics (more common in the Adriatic Sea).

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[8] Species reported from a considerable number of semi-dark caves, at the Mediterranean scale, according to data from the Mediterranean marine cave biodiversity database by Gerovasileiou & Voultsiadou (2012, 2014). Order of species is presented in a decreasing number of records. Each record represents occurrence in the semi-dark zone of a different cave of the Mediterranean Sea.

Facies of erect bryozoans (e.g. *Adeonella* spp. and *Reteporella* spp.) often develop in this biocoenosis (Pérès, 1967; Ros *et al.*, 1985). Finally, the facies of impoverishment are numerous: their composition varies according to the nature of the factor generating the impoverishment of the assemblages (e.g. intense water movement). For example, if the cave is too shallow, many species characteristic of this biocoenosis can be absent, and hydroids (e.g. *Eudendrium armatum*) are particularly developed. High sedimentation rates, causing the excess of mud, can lead to the dominance of erect sponges (especially *Axinella* spp.).

5.3.2. The dark cave biocoenosis

This biocoenosis develops in the inner sectors of the blind-ended caves. The shift from semi-dark to dark cave biocoenosis is evidenced through a sharp decrease in biotic cover, species richness, biomass, three-dimensional complexity (i.e. replacement of erect growth forms by encrusting ones) (Fig. 5.3), and the appearance of a black mineral coating of Mn-Fe oxides on the substrate (Pérès, 1967; Harmelin *et al.*, 1985). Laborel & Vacelet (1959)

described a transitional zone between GSO and GO biocoenoses, where sponges and scleractinians are still abundant but the biotic cover decreases, and a black coating appears on the rock. Nodular and crest-like bryozoan formations (Fig. 5.3) often develop in this transitional zone (Harmelin, 1985; Harmelin *et al.*, 1985), although in some cases they are present in the dark cave biocoenosis (Balduzzi *et al.*, 1989). Bianchi *et al.* (1986), described the most important species of this zone in the Grotta Marina of Bergeggi (Italy).

Harmelin *et al.* (1985) also noticed that the GO biocoenosis could be further sub-divided in two zones, characterized by different biotic covers (50-80% and 10-40%, respectively), while in anchialine caves, two additional zones can occur (i.e. the first one inhabited only by small-sized sponges and scattered serpulids and the terminal one where sessile fauna disappears). However, they highlighted that cave morphology largely influences zonation patterns, and thus, biotic cover in tunnel-shaped caves with constant water movement could reach 100% even in the totally dark zone.
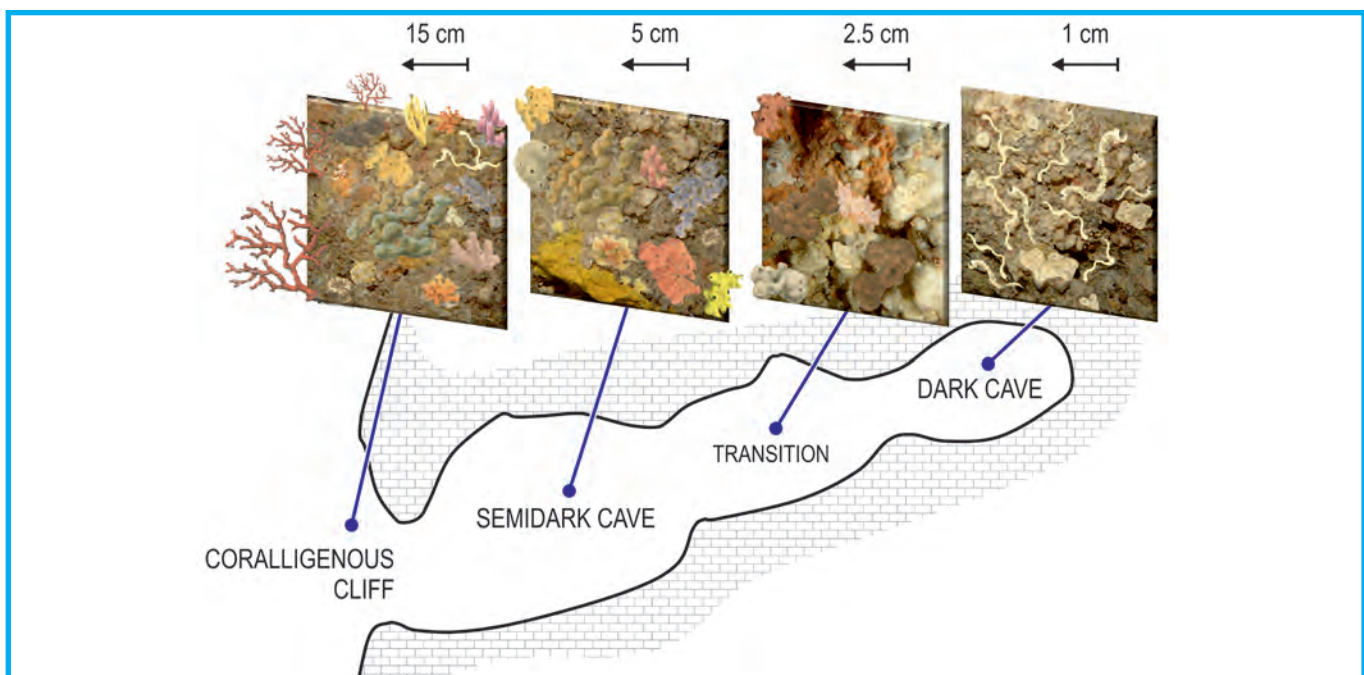
Fig. 5.3. Ecological zonation in a marine cave, depicting: (1) the coralligenous biocoenosis of the cave entrance, (2) the biocoenosis of semi-dark caves, (3) a transitional zone where bryozoan nodules develop, and (4) the dark cave biocoenosis. A marked decrease of three-dimensional complexity, biomass, biotic cover and diversity is evident (Redrawn and modified from Harmelin *et al.*, 1985).

Benthic community in dark cave sectors is usually sparsely colonized by sponges, serpulid polychaetes, bryozoans and brachiopods (Pérès, 1967). The most common sponges are *Petrosia ficiformis* (usually discoloured), *Petrobiona massiliana* (more common in the Western Mediterranean Sea), *Chondrosia reniformis* (usually discoloured), *Diplastrella bistellata*, *Penares*

spp., and *Haliclona mucosa* (Pérès, 1967; Gerovasileiou & Voultsiadou, 2012). Some deep-water species have been recorded in sublittoral dark caves, regardless of depth, such as the hexactinellid (glass) spong *Oopsacas minuta*, which has been reported from caves of Marseille and Croatia (Harmelin *et al.*, 1985; Vacelet *et al.*, 1994; Bakran-Petricioli *et al.*, 2007).

Serpulid polychaetes are among the most dominant taxa in the dark cave biocoenosis, with the typical species being *Serpula cavernicola* and *Spiraserpula massiliensis* (Zibrowius, 1968; Sanfilippo & Mòllica, 2000; Bianchi & Sanfilippo, 2003). The species *Protula tubularia* often forms aggregates which provide the basis for the creation of bioconstructions in the form of "biostalactites". These are constructed by serpulids, sponges, bryozoans, foraminiferans and carbonate-forming microorganisms (Sanfilippo *et al.*, 2015). To date, biostalactites have been discovered in dark caves of Apulia (Onorato *et al.*, 2003; Belmonte *et al.*, 2009), Sicily (Guido *et al.*, 2012, 2013; Sanfilippo *et al.*, 2015), Cyprus (Guido *et al.*, 2017a) and Greece (Sanfilippo *et al.*, 2017; Guido *et al.*, 2019a,b).

Another characteristic type of bioconstructions has the shape of small nodules and sub-parallel crests (approximately 2-3 cm in height), which are often present in the transitional zone between the semi-dark and dark cave biocoenoses, and sometimes further inside the dark cave zones. These formations result from the concretion of several bryozoans (e.g. *Onychocella marioni* and *Hippaliosina depressa* – the latter mainly in the Eastern Mediterranean Sea) and other encrusting taxa (e.g. corals, brachiopods, serpulids, and agglutinate foraminifers), creating a vertical microstratification (Harmelin *et al.*, 1985; Rosso *et al.*, 2019). Such formations have been described from marine caves of Marseille (Harmelin, 1985, 2000, 2003), Sicily (Rosso *et al.*, 2013b, 2015) and the Greek Islands of the Aegean and Ionian seas (Rosso *et al.*, 2019; Gerovasileiou, unpublished data), with those of the latter areas being smaller in size compared to those of Marseille. Brachiopods (e.g. *Joania cordata*, *Argyrotheca cuneata*, and *Novocrania anomala*) are common in dark caves (Logan *et al.*, 2004). The species *N. anomala* is often found in high numbers, cemented on cave walls and ceilings (Logan *et al.*, 2004; Radolović *et al.*, 2015; Rosso *et al.*, 2019), sometimes being part of the above bioconstructions.

Several motile species often find shelter in dark caves, such as the mysids *Hemimysis margalefi* and *H. speluncola*, the decapods *Stenopus spinosus*, *Palinurus elephas*, *Plesionika narval* (more frequent in Southern and Eastern Mediterranean areas), *Galathea strigosa* and *Herbstia condyliata*, and the fish species *Apogon imberbis* and *Grammonus ater* (Pérès, 1967; Ros *et al.*, 1985, Bussotti *et al.*, 2015; Gerovasileiou *et al.*, 2015b).

5.4. Soft substrate communities

Cave sediments are usually muddy, thus resembling certain deep (circalittoral or bathyal) soft bottoms, but they often include a coarse fraction, made of either mineral, coming from the outside, or biogenic, originating from fallen fragments of skeletons and calcareous shells of the organisms (e.g. bryozoans, scleractinians, serpulids, brachiopods and molluscs) present on the cave walls and ceiling (Monteiro-Marques,

1981; Bianchi & Morri, 2003; Rosso *et al.*, 2013a). In the Grotta Marina of Bergeggi (Italy), for example, the sediments consist essentially of gravel near the outside and in the tunnel-shaped sectors, and of fine sand and mud in more internal and terminal sectors (Bianchi *et al.*, 1986). Thus, cave floors can represent an enclave of soft bottom within the rocky coastal system.

However, soft substrate communities of Mediterranean marine cave floors have not been studied as intensively as those of hard substrates, and there is very little information on their composition or their affinities with their counterparts living outside the caves. A recent overview of 307 studies on Mediterranean marine caves showed that only 15% provided – at least – some information on soft substrate biodiversity (including single species records, e.g. *Cerianthus membranaceus*) (Gerovasileiou & Voultsiadou, 2014). According to the same overview, a total of 332 taxa have been recorded in cave sediments, mainly bryozoans (79 taxa on detached fragments, probably including non-living material), polychaetes (59 taxa), bivalves (48 taxa, although it was not always specified if they were found living or dead), amphipods (33 taxa), tardigrades (31 taxa), copepods (23 taxa) and Gastrotricha (16 taxa).

A small number of studies specifically focused on the structure of soft sediment fauna in marine caves of France, Italy and Spain (Monteiro-Marques, 1981; Akoumianaki & Hughes, 2004; Todaro *et al.*, 2006; Navarro-Barranco *et al.*, 2012, 2013a,b, 2014; Janssen *et al.*, 2013). The above studies showed that the structure of soft-bottom communities inside marine caves is difficult to predict or generalize.

5.4.1. Macrobenthos
Monteiro-Marques (1981) studied the soft sediment macrofauna in three caves of the Marseille region (Grotte du Figuier, Grotte des Trémies and Grotte de Jarre) and found 27 species (11 polychaetes, 10 molluscs, 3 sipunculids, 2 echinoderms and 1 crustacean). Interestingly, the most abundant species was the sipunculid *Onchnesoma steenstrupii*, otherwise reported from bathyal muds. The assemblage was characterized by species linked to heterogeneous sediments, rich in coarse elements, such as the bivalve *Gouldia minima* and the polychaete *Aponuphis bilin eata*. However, the abundance of several indicator taxa of unstable environmental conditions was noted, such as the bivalve *Corbula gibba* and the polychaetes *Spio multioculata* and *Lumbrineris latreilli*.

Akoumianaki & Hughes (2004) studied the distribution of macroinfauna in a very peculiar cave, Grotta Azzurra of Capo Palinuro (Italy). Its peculiarity derives both from the presence of sulphur hydrothermal springs, mainly located in the inner dark chamber (known as "Sala della Neve" = Snow Hall) of the cave (Southward *et al.*, 1996) and from the efficient water exchange allowed

by the large dimensions and the width of the entrances (Bianchi *et al.*, 1998 – see chapter 4). A total of 97 species were recorded, specifically 55 polychaetes, 17 molluscs, 12 crustaceans, 4 sipunculids, 2 echinoderms, and 7 other taxa (Anthozoa, Oligochaeta, Nemertea, Pycnogonida, Enteropneusta, Brachiopoda, and Ascidiacea). In all sampling stations, polychaetes dominated in terms of both abundance and species richness. The most abundant species in the cave sediment were the polychaete *Levinsenia gracilis* (62%), the sipunculid *Onchnesoma steenstrupii* (14.6%), the polychaete *Paradoneis lyra* (7.2%) and the ophiurid *Amphiura chiajei* (4.9%). Species richness and density varied across cave sectors, indicating differences at a scale of few metres. However, there was no clear inward decline of abundance, biomass or diversity, suggesting that the chemosynthetic inputs in the inner cave chamber (Snow Hall) provide an additional trophic supply, thus having a positive effect on benthic assemblages. The presence of taxa which are considered as indicators of environmental instability in high abundances (e.g. the polychaetes *P. lyra*, *L. gracilis* and several species of the family Capitellidae, and the bivalves *Corbula gibba* and *Thyasira flexuosa*) indicated the excess of organic matter enrichment, similarly the sediments in marine caves of Marseilles (Monteiro-Marques, 1981).

In addition to the infauna, an abundant epifauna (fixed or sedentary) was found in the Snow Hall, such as the bivalve mollusc *Pinna nobilis*, the tubiculous polychaetes *Phyllochaetopterus socialis* and *Sabella pavonina*, the echinoderms *Antedon mediterranea*, *Stylocidaris affinis* and *Ophioderma longicaudum* (Bianchi & Morri, 2003). Bianchi *et al.* (1994) suggested that this unusual abundance of filter-feeding or detritivorous epifauna was related to the chemosynthetic production by the sulphur bacteria in this particular environment.

Certain large tube-dwelling or digging anthozoans can be also common on the sedimentary bottoms of marine caves (Morri *et al.*, 1991). *Cerianthus membranaceus* is known from several Mediterranean caves. *Arachnanthus oligopodus* has been reported in the Grotta delle Corvine, in Salento (Denitto *et al.*, 1999). A population of *Halcampoides purpureus* is known from the Cave of Cala di Mitigliano, in the Tyrrhenian Sea (Boero *et al.*, 1991).

The most recent studies about soft substrate macrofauna in Mediterranean marine caves took place in the coasts of Granada (Alboran Sea, Spain). Navarro-Barranco *et al.* (2013a,b, 2014) investigated six caves which covered a wide depth range (6-30 m), and compared the crustacean fauna in sediments of the caves' interior and adjacent external sites. None of the species exhibited a significant preference to cave stations, although amphipods of the genus *Harpinia* dominated inside the marine caves. In all caves, external sediments had higher species richness and

a significant decline in diversity values was found inside the caves. However, this was not the case for abundance, which decreased only in deeper caves, while in the shallower ones the number of individuals was lower outside caves. This is possibly related to the fact that shallow caves provide a more stable environment, protected from waves, winds and storms which affect the exposed external sites. In addition, while the structure of the crustacean assemblage in external sites was quite similar (47.4% Bray-Curtis similarity), internal cave sites showed high variability and strong individuality (4.9% Bray-Curtis similarity), suggesting that these assemblages are influenced by many and complex factors (e.g. sediment granulometry, heavy metals concentration, organic matter and nitrogen concentration).

5.4.2. Meiobenthos
Meiobenthos has been rarely studied in Mediterranean marine caves. Specifically, only a few studies have investigated spatial variability of meiofauna, on soft (Todaro *et al.*, 2006; Janssen *et al.*, 2013) and hard substrates (Russo *et al.*, 2015), while taxonomic studies have brought to light several new species of tardigrades, gastrotrichs and a priapulid, possibly having deep-sea affinities (Zeppilli *et al.*, 2018 and references therein; also see chapter 6). In addition, a recent study has investigated the distribution of benthic foraminifera in a marine cave of Sardinia (Romano *et al.*, 2018).

Todaro *et al.* (2006) studied meiofauna in three dark sites of the Grotta di Ciolo (Salento, Italy), at 55, 75 and 90 m from the entrance. A high diversity was found, including representative taxa of 12 major groups, with a total density of 656 and 1069 individuals·10 cm^{-2} in November and June, respectively. Nematodes were the most abundant taxon, followed by harpacticoid copepods, priapulids, polychaetes and gastrotrichs, which were found in both seasons. Turbellarians, nemertines, ostracods, tanaids, oligochaetes, tardigrades and amphipods were also found, but with very low densities and/or sporadically. The community structure was quite different along the cave sites (e.g. priapulids were the second most abundant taxon in the first station), with small seasonal variation. Mean density of the total meiofauna decreased inwards, and particularly of harpacticoid copepods, thus indicating that meiobenthic community is structured in accordance with the trophic depletion hypothesis.

More recently, Janssen *et al.* (2013) studied the meiofauna of the sediments of the 3PP Cave (Marseille, France) at three sampling stations (entrance, middle, and blind end). Meiofauna was assigned to 14 major taxa. Nematodes were the most abundant taxon, followed by copepods, priapulids and annelids. Kinorhynchs, ostracods, tardigrades, and rotifers were also observed but in lower numbers. Six other taxa (i.e. Acari, Amphipoda, Bivalvia, Gastrotricha, Isopoda, and Loricifera), were represented

by single specimens. The community composition, based on presence/absence of major taxa, did not vary among stations. Nevertheless, individual densities and copepod diversity decreased inwards, and tardigrades were restricted to the inner parts of the cave. Copepods were assigned to 27 families and 90 species, 75% of which were new to science. There were significant quantitative and qualitative differences in the composition of copepod assemblages between the three stations, at the family, genus, and species levels. Interestingly, some harpacticoid taxa, known from the deep sea (e.g. *Marsteinia*, *Ancorabolina*, *Paranannopus*, *Nematovorax*, and Argestidae), were recorded in the cave, and the assemblage of the inner cave end was classified as "abyssal", highlighting the faunal affinities between marine caves and the deep sea. The meiofauna of the sediments of two caves in Ustica Island (Sicily, Italy) was poorer and scarcer than the one outside the cave, and included different taxa (Ape *et al.*, 2016). Nematodes, in particular, were represented in the dark sections of the caves by exclusive species (e.g. *Anticoma acuminata*). Availability of organic matter (i.e. phytopigment concentration) influenced meiofaunal distribution and composition inside the caves, while bacteria represented the most important food source for nematodes.

Romano *et al.* (2018) studied the diversity and distribution of benthic foraminifera along the marine cave Bel Torrente in Sardinia. Benthic foraminifers were found along the first 330 m of the cave, while the inner sectors were totally barren. A total of 106 species were found, of which 76 were represented both by dead and living specimens. The most abundant species were *Gavelinopsis praegeri*, *Reophax dentaliniformis*, *Eggerella advena* and *Ammonia inflata*. Density and species diversity were negatively correlated with the distance from the entrance and the associated environmental gradients, indicating increasing environmental stress inwards. Salinity was found to affect the assemblage structure, while water acidification was suggested to cause a shift from a calcareous hyaline-dominated assemblage to an agglutinant-dominated one, occurring at 120-150 m from the entrance. Common taxa from external coastal marine areas were found only close to the entrance, while species found inside the cave were exclusively epifaunal clinging/attached or opportunist infaunal taxa, which tolerate a wide variability of environmental parameters, possibly generated by episodic water floods.

The encrusting sponge *Spirastrella cunctatrix* on a semi-dark cave wall.
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6. ECOSYSTEM FUNCTIONING

6.1. Trophic depletion

Marine cave environments are based on pure secondary production due to the lack of light and the sub-sequent absence of photo-autotrophic organisms (Riedl, 1966). Therefore, marine cave communities depend completely on the input of matter and energy from external environments. By drawing their nourishment from the water column, filter-feeders (active and passive) are the secondary producers that deal with transferring matter and energy from the outside, where they were produced, to the inside, where they will be processed and consumed (Ott & Svoboda, 1978; Bibiloni et al., 1984; Balduzzi et al., 1989; Bianchi, 1994; Rastorgueff et al., 2011, 2015a). This explains their quantitative dominance, which is a typical feature of all marine caves (Ott & Svoboda, 1978; Bibiloni et al., 1984). The maintenance of the marine cave ecosystem greatly depends on the input of suspended particulate organic matter in the water, which in turn depends on the water exchange in the cave (see chapter 4). Thus, the most confined caves or cave sectors will have much lower food availability (oligotrophy), and consequently, an impoverished community in terms of species richness, biotic cover / abundance and biomass (Harmelin et al., 1985; Zabala et al., 1989; Fichez, 1990b; Bianchi & Morri, 1994; Bianchi et al., 1996). Trophic depletion makes ecosystems in confined dark caves highly oligotrophic, similar to those of the deep sea (Harmelin et al., 1985). The inwards reduction of trophic input is not only quantitative but also qualitative (Bianchi & Morri, 1999).

6.1.1. Decrease in food quantity
The amount of total particulate matter, as well as the organic carbon and nitrogen it contains, decrease significantly from the semi-dark to the dark zone of marine caves (Bianchi et al., 2003). This decrease occurs both directly, due to the progressive sedimentation of the suspended particles, and indirectly, through their capture by passive filter feeders (Fichez, 1991c; Palau et al., 1991; Garrabou & Flos, 1995; Rastorgueff et al., 2011, 2015a). The abundance of the filter feeders on cave walls and ceilings is responsible for the decrease in the content of carbohydrates, lipids and proteins in the innermost cave zones. The water that reaches these areas has lost more than half of its original content of organic matter, and thus, the suspended particles reaching these areas do not provide sufficient energy to support an abundant benthic fauna. This state can change during the spring season, when the warming of the open sea generates a rapid mixing of the waters with concomitant new entries of organic matter, in particular of phytoplankton (Fichez, 1989, 1990b). The importance of phytoplankton in the suspended particulate material that penetrates into the cave can be easily deduced from the measurement of the concentration of chlorophyll-a in the water. In fact, in the absence of light, it cannot increase, while its decrease represents a direct index of trophic depletion. The measurements carried out in the Grotta Marina of Bergeggi by Morri et al. (1994a) showed that the concentration of chlorophyll-a remains close to the typical values of the external marine environment near the entrance; it decreases slightly in the tunnel section, and more markedly in the blind-ended chambers of the cave, reaching very low values in the inner lakes. In this case, therefore, trophic depletion seems to overlap perfectly with the hydrological confinement gradient (Bianchi & Morri, 1994).

6.1.2. Degradation of food quality
Moving from a semi-dark cave to a dark cave, not only the total amount of organic matter is reduced, but also its composition changes. This change takes place in the sense of a reduction in the nutritional value of organic matter and can be highlighted with:

• The ratio between the carbon content and the nitrogen content (C/N ratio), which is an index of the food value of the organic matter. Food with high carbon and little nitrogen content (e.g. cellulose) is poorly nutritious compared with food that is proportionally richer in nitrogen (e.g. proteins). Both in the Grotte des Trémies (Marseille, France) and in the Grotta Marina of Bergeggi (Liguria, Italy), the C/N ratio tends to increase inwards, indicating a decrease in the food value of the suspended particulate matter (Morri et al., 1994a). In both caves, the C/N ratio is lower than 17, a threshold value for animal consumption (Russel-Hunter, 1970). The study of the C/N ratio in the suspended particulate matter of two marine caves of Marseille by Rastorgueff et al. (2011) showed that the ratio had higher values at the entrance of Jarre Cave compared to the mid-cave and cave end, due to the rapid accumulation of organic matter (seagrass and macroalgal detritus) just after the entrance. In 3PP Cave, the high C/N value inside the cave indicated the accumulation of refractory material close to the cave end. Regarding the C/N ratio in the particulate organic material, there were no differences between the outside and internal waters of the two caves, indicating a rather fresh organic material, but in lower quantity inside the caves.

• The ratio between simple and complex organic matter can be halved in the inner cave sectors, indicating a sharp decline in the quality of food available to consumers. Specifically, while the quantity of carbohydrates, proteins and lipids, which form an easily degradable fraction of the organic matter, decreases inwards, the proportion of hetero-poly-condensates, geopolymers, marine humic substances and other complex organic molecules, very resistant to degradation, increases (Bianchi et al., 2003).

• The ratio between the amount of chlorophyll and that of phaeophytin represents a further index of the quality of the suspended organic substance. In dark marine caves, chlorophyll is short-lived and rapidly degrades to phaeophytin. Thus, high values of this ratio will characterize "fresh" organic matter, rich in live phytoplankton cells, while lower values indicate particulate matter composed mainly of organic detritus (Fichez, 1990c). Between the semi-dark and the dark cave zones, the chlorophyll/phaeophytin ratio can decrease by two orders of magnitude, indicating the qualitative degradation of the food available to consumers inwards (Bianchi *et al.*, 2003).

6.1.3. Strategies to mitigate trophic depletion

Cave biota respond to trophic depletion with a series of adaptations. Some species present physiological adaptations, such as scarce food specialization, allowing the exploitation of all possible resources, and resistance to starvation, which allows the survival under an irregular and unpredictable food intake (Bibiloni *et al.*, 1984; Culver, 1985). In addition, there are also strategies regarding the functioning of the entire cave ecosystem, rather than the physiological response of individual species. According to Bianchi *et al.* (2003) three principal mechanisms can be identified: (a) nychthemeral migrations; (b) epibiosis and phoresy; and (c) chemolithoautotrophy.

6.1.3.1. Nychthemeral migrations

Motile species exhibiting nychthemeral migration patterns significantly affect the flow of energy in the marine cave ecosystem since they mitigate oligotrophy by importing organic matter. Specifically, some stygoxene species of crustaceans and fish find shelter within caves during daytime but come out at night in order to seek for food in nearby external habitats. This role has been studied mostly in swarm-forming mysids and in the cardinal fish *Apogon imberbis* (Riera *et al.*, 1991; Coma *et al.*, 1997; Rastorgueff *et al.*, 2011, 2015a,b; Bussotti *et al.*, 2017, 2018). Different species of mysids form swarms of different sizes; for instance, *Hemimysis speluncola* forms swarms of millions of individuals, *Hemimysis margalefi* of thousands of individuals, while *Hemimysis lamornae mediterranea* can gather tens to hundreds of individuals (Rastorgueff *et al.*, 2015a and references therein). During their stay in the cave, they release faecal pellets which increase the internal trophic load, thus mitigating trophic depletion (Coma *et al.*, 1997; Rastorgueff *et al.*, 2011). In addition to the above role, they can be preyed upon by sessile carnivores, such as the sponge *Lycopodina hypogea* (Vacelet & Boury-Esnault, 1995; Rastorgueff *et al.*, 2011, 2015b), the actiniarian *Halcampoides purpureus* (Boero *et al.*, 1991), and cerianthids (Rastorgueff *et al.*, 2011, 2015a). Recent studies have shown that the cardinal fish *A. imberbis*, which is the most abundant (up to 1800 individuals 100 m^{-2}) and common fish in Mediterranean marine caves (Bussotti *et al.*, 2002, 2003, 2015, 2017, 2018), can also be an important vector of organic matter mitigating trophic depletion inside caves. It shelters inside caves during day and moves outside at night in order to feed on small invertebrates (e.g. crustaceans and annelids) in rocky beds and *Posidonia meadows*.

6.1.3.2. Epibiosis and phoresy

Large decapod crustaceans that carry out nychthemeral migrations between the cave and the external marine environment also create an opportunity for transport (phoresy) for sessile organisms. The crab *Dromia personata*, for example, is commonly called "sponge crab" due to its habit of carrying on its carapace fragments of sponges (in caves usually *Chondrosia reniformis* and *Petrosia ficiformis*). Many other small sessile taxa can be also installed as epibionts on its carapace, such as serpulids, bryozoans and barnacles. These sessile filter feeders, thanks to the phoretic transport, can also "get out" to feed during night outside, thus bypassing the hydrological confinement gradient and avoiding the trophic depletion conditions inside caves. It should be noted that these epibionts, in addition to participating in the horizontal transfer of organic matter, can form a source of larvae capable of maintaining pseudo-populations of stygophilic taxa in caves, thus contributing to their biodiversity (Bianchi *et al.*, 2003).

6.1.3.3. Chemo-litho-autotrophy

Exploration of Mediterranean marine caves brought to light caves with sulphidic hydrothermal springs in Capo Palinuro, Tyrrhenian Sea (Abbiati *et al.*, 1992, 1994). These springs convey water full of sulphurs which, being warm, unsalted, and therefore less dense, floats over the seawater, and accumulates in the vault of caves. At the interface between the marine water layer and the hydrothermal waters, a permanent chemocline is formed. The walls, vault and even the sediment of the cave bottom are populated by well-adapted prokaryotes (*Beggiatoa*), which form extensive biofilms/mats and are responsible for oxidizing sulphides in sulphates (Mattison *et al.*, 1998; Canganella *et al.*, 2002, 2007). From this oxidation sulphur bacteria draw energy for their metabolism, which is therefore definable as chemo-litho-autotrophic. Thus, there is a primary source of production, not photosynthetic, but native to the cave, similar to what has already been seen in some terrestrial caves (Sarbu *et al.*, 1996).

Chemo-litho-autotrophic production inside these caves mitigates the trophic depletion. The profound influence that the sulphur bacterial production has on the marine cave ecosystem has been mostly studied in the Grotta Azzurra (Italy). This production constitutes 31% of the available total particulate organic matter, thus representing an additional source of food and energy for a benthic community of consumers that is indeed unusually rich and abundant (Abbiati *et al.*, 1992; Cinelli *et al.*, 1994; Bianchi *et al.*, 1994; Southward *et al.*, 1996; Airoldi & Cinelli, 1997). Some species of sessile filter feeders, such as the sponge *Geodia cydonium* and the

scleractinian *Astroides calycularis*, exhibit gigantism, which is probably related to the greater availability of food (Morri *et al.*, 1994b). Other sessile taxa, such as the polychaete *Phyllochaetopterus socialis* and the hydroid *Eudendrium armatum*, maintain bacteria near their feeding appendices. Motile species, such as the sea urchin *Arbacia lixula* and the nudibranch *Doriopsilla areolata*, cross the chemocline, penetrating for short stretches in the anoxic waters above, to graze on sulphur bacterial filaments. The consumers dwelling on the cave bottom, which are either filter feeders (e.g. the polychaete *Sabella pavonina*, the bivalve *Pinna nobilis* and the crinoid *Antedon mediterranea*) or detritivores (e.g. the ophiurid *Ophioderma longicaudum*), also take advantage of the "marine snow" of bacterial organic matter that falls from the ceiling in the form of white flakes (Bianchi *et al.*, 2003).

During a recent study on the marine cave biodiversity of the National Marine Park of Zakynthos (Ionian Sea, Greece), several marine caves (semi- and entirely submerged), small cavities and fissure systems located at a depth range of 0-25 m, were found to be densely colonized by egg-shaped, foam-shaped and filamentous microbial structures, that were characterised by a strong smell of hydrogen sulphide gas (Polymenakou *et al.*, 2018). Anaerobic enrichment cultures indicated strong methanogenesis. The studied caves were sparsely colonized by sessile invertebrates, but during underwater observations it was noted that some fish were feeding on white microbial aggregates drifted by the exhalant water flowing from cavities and fissures (Gerovasileiou, unpublished data). Further study is required in order to investigate the trophic structure and function of these ecosystems, which are probably more widespread than previously known.

6.1.4. Analogies with deep-sea ecosystems

The export of organic matter from marine caves to external environments is rather insignificant, as are the sedimentation losses. All – or at least the greatest part of – the organic material present in marine caves is processed and remineralized through aerobic processes[9], with the maximal efficiency (Fichez, 1990b, 1991a,c; Bianchi *et al.*, 1996). This characteristic makes marine caves an exemplary oligotrophic (Fichez, 1990a,b,c) and heterotrophic (Riedl, 1966) ecosystem, similar to deep-sea ecosystems (Fichez, 1989), where – in the absence of light and primary production – matter and energy are imported from shallower habitats due to floating or gravity (Bianchi *et al.*, 2003).

In addition, in those marine caves which have sulphur springs, the dependence of their ecosystem on chemo-litho-autotrophic production resembles ecosystems that exist at great depth in the vicinity of hydrothermal vents on mid-oceanic ridges (Bianchi *et al.*, 2003). There are several other aspects that marine cave ecosystems have in common with those of the deep sea (Zibrowius, 1971; Harmelin *et al.*, 1985; Boury-Esnault *et al.*, 1993; Vacelet *et al.*, 1994; Harmelin & Vacelet, 1997). One of the most characteristic examples is the formation of metal patinas and nodules, essentially iron and manganese oxides, which give blackish colour to the rocks and walls of the more confined dark sectors of submerged caves (Laborel & Vacelet, 1958; Bianchi *et al.*, 1986; Allouc & Harmelin, 2001). Their formation is probably related to bacterial metabolism, under particular physico-chemical conditions which characterize both the deep-sea and the cave environments. Therefore, confined dark caves constitute an easily accessible model or "mesocosm" for the study of deep marine ecosystems, which occupy over half the surface of our planet.

6.2. Trophic organisation

Theoretical models on the functioning and trophic structure of Mediterranean marine cave ecosystems have been developed by Ott & Svoboda (1978), Russo & Bianchi (2003) and recently by Rastorgueff *et al.* (2015a) (Fig. 6.1). Organic matter supply in marine caves consists of suspended organic matter (SOM), dissolved organic matter (DOM) and particulate organic matter (POM), which is usually a mixture of phytoplankton, land-derived and anthropogenic material carried to the sea by river runoff and sewage outflow or even matter originating from terrestrial systems percolating through the cracks and fissures of bedrock (Rastorgueff *et al.*, 2011, 2015a). A further contribution comes from motile organisms (i.e. crustaceans and fish) which move outside-inside caves, either on a nychthemeral or occasional basis, leaving their faecal pellets or their remains (see sub-section 6.1.3.1 and Fig. 6.1).

Cave biota are subjected to an aperiodic food intake which results in lack of specificity for food, high resistance to fasting (as an adaptive response to food shortages) and strong competitiveness for space (e.g. the search for the best sites for filtration) (Bibiloni *et al.*, 1984 ; Culver, 1985). As explained before, primary producers are absent from inside marine caves, and thus the ecosystem includes the following trophic-behavioural categories (Ott & Svoboda, 1978; Russo & Bianchi, 2003; Rastorgueff *et al.*, 2015a): (1) secondary producers (passive and active filter feeders); (2) consumers (characteristic and associate carnivores); (3) detritus feeders and omnivores; (4) migrants; and (5) decomposers. Detailed information about each category is presented below.

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[9] Fichez (1991a) measured benthic oxygen uptake and carbon cycling in the Grotte des Trémies (Marseille, France) and found that while in the outer semi-dark zone of the cave anaerobic pathways accounted for 14% and aerobic pathways for 86% of the total benthic metabolism, the inner dark zone was a strongly carbon-limited ecosystem, where degradation of organic carbon occurred only through aerobic processes. In addition, the low respiration rates in the dark end of the cave were similar to values recorded in oligotrophic deep-sea environments (1000-2000 m depth).
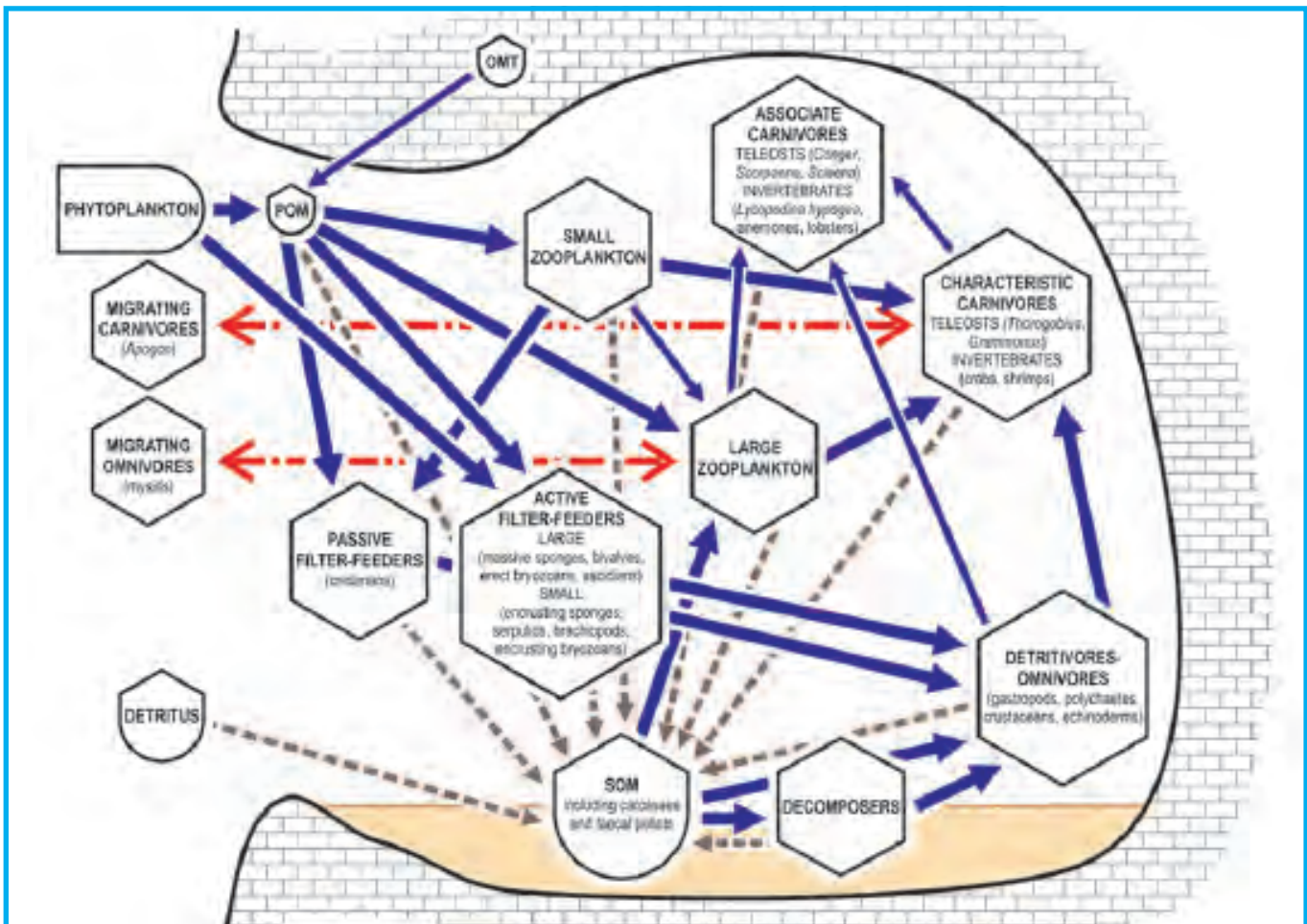
Fig. 6.1. Theoretical model of structure and functioning of the Mediterranean marine cave ecosystem.
Semi-dark and dark cave biocoenoses are indicated for each component of the ecosystem (in boxes).
Black arrows denote the intensity of organic matter fluxes, with major fluxes represented by solid black arrows.
Vertical dashed arrows represent the organic matter which reaches the cave bottom, such as organic matter of terrestrial origin (OMT),
suspended particulate organic matter (POM), faecal pellets and carcasses of dead organisms.
Horizontal dashed arrows indicate major inputs of organic matter into caves either by advection due to water movement
(for POM and detritus) or through nychthemeral horizontal migration of mysids and the cardinal fish Apogon imberbis.
Redrawn and modified from Rastorgueff *et al.* (2015a).

6.2.1. Secondary producers

These are sessile animals that live by drawing directly from the organic matter imported from outside. They are either suspension feeders (also known as passive filter feeders, e.g. cnidarians) or active filter feeders (i.e. sponges, bivalve molluscs, serpulid polychaetes, bryozoans, brachiopods, and ascidians). The main food resource of these taxa is plankton as well as non-living organic substance in suspension. Passive filter feeders require a higher water flow, providing nutritive particles, and thus, they are more abundant at the cave entrance and cave sectors with considerable hydrodynamics, such as cave ceilings, which are characterized by more turbulent water movement (Gili & Ballesteros, 1991; Russo & Bianchi, 2003). Thus, their distribution towards inner cave sectors is limited by water confinement, except for tunnel-shaped caves (Bianchi & Morri, 1994). Active filter feeders are the most common and widespread taxa inside marine caves as they are less dependent on the advection of nutritive particles (Rastorgueff *et al.*, 2015a). Many of them are colonial or modular and

exhibit a wide variety of growth forms (Gerovasileiou *et al.*, 2017). The dominance of particular growth forms in particular cave sectors reflects an adaptation to water confinement and trophic depletion. For instance, it has been suggested that the dominance of thin encrusting sponges towards the oligotrophic inner cave sectors, is related to the fact that they present a more effective filtration surface/volume ratio, and thus, they can exploit the rare particulate organic matter of the water (Biboloni *et al.*, 1989). All in all, secondary producers constitute the main trophic level in terms of both biomass and species richness in marine caves and represent the trophic substrate necessary for higher order consumers.

6.2.2. Consumers

These are animals that feed on the organic matter produced inside the cave and coming mainly from the previous level of the secondary producers. Herbivores (grazers) are generally absent from caves, due to the absence of primary producers, although echinoids coming from the nearby algal-dominated communities can frequently be observed (Harmelin *et al.*, 1985; Russo

& Bianchi, 2003). The carnivores to be found in caves include both sessile and motile forms. Several motile carnivores are encountered in caves (stygophiles and stygoxenes). These can be further categorized into characteristic carnivores, which are frequently observed in caves, although they also occur in other shadowy/dark habitats, and associate carnivores, which occasionally find refuge in caves but are not characteristic of this habitat (Rastorgueff *et al.*, 2011, 2015a). The first category includes many fish species, such as the cardinal fish *Apogon imberbis*, gobies (e.g. *Thorogobius ephippiatus* and *Gammogobius steinitzi*), the scorpion fish *Scorpaena notata*, the brotulid *Grammonus ater*, and decapods (e.g. *Herbstia condyliata*, *Lysmata seticaudata*, *Lysmata nilita*, *Palaemon serratus*, *Plesionika narval*, and *Stenopus spinosus*). The associate carnivore category also includes fish species (e.g. *Conger conger* and *Phycis phycis*), decapods (e.g. *Homarus gammarus*, *Palinurus elephas* and *Scyllarides latus*) and anemones (e.g. *Arachnanthus oligopodus* and *Cerianthus membranaceus*). The presence of sessile carnivores (e.g. the cladhorizid sponge *Lycopodina hypogea*, the anemone *Halcampoides purpureus* and cerianthids) is linked to their predation on populations of small motile taxa, such as mysids, which perform nychthemeral horizontal migrations between the cave and the outside (Russo & Bianchi, 2003; Rastorgueff *et al.*, 2011, 2015a,b).

Regarding macroinfauna, the study of the gut content of soft substrate amphipods inside and outside six marine caves of Granada (Alboran Sea, Spain) showed that carnivores represented almost 60% of the amphipod species and over 80% of the abundance inside caves (Navarro-Barranco *et al.*, 2013b). On the other hand, detritivorous amphipods were absent from cave sediments, while they dominated in adjacent external sediments. The study of the macroinvertebrate fauna associated with two massive-tubular sponges (*Agelas oroides* and *Aplysina aerophoba*) in two marine caves of Lesvos Island (Aegean Sea, Greece) by Gerovasileiou *et al.* (2016a) showed that carnivores (basically crustaceans) dominated in terms of abundance in both sponges (especially the amphipod *Colomastix pusilla*). While carnivores dominated in terms of species richness in *A. aerophoba*, deposit-feeders (mainly polychaetes) was the species-richest feeding group in *A. oroides*. The trophic structure of the sponge-associated macrofauna did not change significantly across different cave sectors.

6.2.3. Detritus feeders and omnivores

Detritus feeders and omnivores constitute an important component of the food chain in the marine cave ecosystem, as they make the organic matter that is trapped in the detritus available to other cave dwellers; therefore, detritus constitutes an additional food source to cope with the trophic depletion in marine caves (Rastorgueff *et al.*, 2011, 2015a). In Mediterranean marine caves detritus feeders and omnivores are represented by decapod crustaceans (e.g. *Herbstia condyliata*, *Galathea strigosa*, and *Scyllarus arctus*), gastropods, motile polychaetes and echinoderms.

6.2.4. Migrants

As previously described, swarm-forming mysids and fish exhibiting nychthemeral migrations inside-outside caves have a pivotal role in mitigating trophic depletion (see sub-section 6.1.3.1). In addition to mysids and the cardinal fish, other motile species, including characteristic and associate carnivores that find refuge in caves, move outside at night in order to feed in the open coastal waters, such as decapod crustaceans (e.g. *Plesionika narval*, *Palinurus elephas*, *Scyllarus arctus*, *Homarus gammarus*), cephalopods (e.g. *Octopus* spp.) and fish (*Phycis phycis*, *Sciaena umbra*, serranids, sparids, gobies, etc.). The presence of such migrant populations, sometimes in high abundances, can represent an important import pathway for organic matter from the outside in the form of faecal pellets, determining in certain cases local conditions for trophic improvement (Bianchi & Morri, 1994; Russo & Bianchi, 2003), but, in the overall budget, it can also represent an energy loss for the cave system.

6.2.5. Decomposers

Little is known about decomposers (bacteria, fungi and protozoa) in marine caves, despite their very important role in the ecosystem. For example, it has been calculated, that their activity produces more than 80% of the energy available in the sediments of the cave bottom (Smith *et al.*, 1972; Zabala *et al.*, 1989; Fichez, 1991a). Important microbial mats (i.e. sulphur bacteria and mixotrophic Chrysophyceae) may develop on organic-rich sediments that accumulate in caves following disturbances (Nepote *et al.*, 2017).

6.3. Other biotic interactions

6.3.1. Spatial inter-specific competition

The dramatic environmental gradients which characterize marine caves impose a strong environmental filtering of ecological traits of the biota. Benthic taxa with similar ecological traits co-occur and functionally resemble each other in their need to respond to the same parameters; this indicates that the cave ecosystem sustains a high degree of functional redundancy, thus maintaining important ecosystem processes (Gerovasileiou *et al.*, 2017). The dispersal of propagules and larvae from their parental habitats (inside or outside caves), is not only determined by environmental parameters (e.g. water movement) but also by larval behaviour (e.g. swimming efficiency and phototaxis) and by a differential post-settlement survival of taxa against various environmental factors (e.g. light, food availability, and spatial competition) (Benedetti-Cecchi *et al.*, 1997; Mariani *et al.*, 2006; Denitto *et al.*, 2007; Moscatello & Belmonte, 2007). This results in a marked spatial variability of benthic community structure and function.

Competitive interactions between different organisms significantly contribute to this spatial variability, at smaller spatial scales (e.g. different cave sectors and micro-habitats), where species compete for the limited available resources (Gerovasileiou et al., 2017). One of the most characteristic examples of competition concerns availability for living space, especially at the transitional zone between the well-lit cave entrance and the semi-dark cave zone. The gradual elimination of light with increasing distance from the entrance leads to the disappearance of photosynthetic macroalgae (primary producers)[10] and the development of characteristic cave communities, dominated by sciaphilic sessile animals (Pérès & Picard, 1949; Riedl, 1966; Cinelli et al., 1977; Balduzzi et al., 1989; Corriero et al., 2000; Martí et al., 2004a; Gerovasileiou et al., 2017).

The production of bioactive chemical compounds is a common defence strategy in sessile benthic taxa. Uriz et al. (1991) studied chemically mediated bioactivity in several types of benthic communities in the Balearic Archipelago and the Columbretes Islands and found that sciaphilic/cryptic communities (i.e. the lower side of coralligenous blocks and semi-dark caves) harboured the highest number of bioactive species (mainly sponges, bryozoans and tunicates). The study of chemical natural toxicity in sponges, cnidarians, bryozoans and tunicates of two caves in the Medes and Cabrera Islands (Martí et al., 2005; Turon et al., 2009) showed that all phyla considered included high numbers of toxic representatives. Toxicity varied significantly with season and/or cave community for sponges, cnidarians and bryozoans, although no common patterns were found for the two caves. The studied tunicates remained toxic in all seasons and communities. In the cave of Cabrera Island, the highest mean bioactivity for sponges was recorded in the innermost cave sector in spring. However, the highest number of bioactive sponges was found in the semi-dark cave community. The higher number of non-bioactive sponges in the dark cave community is possibly related to the fact that there are less inter- specific contacts, due to the higher space availability. The most toxic species were the encrusting sponge Crambe crambe and the ascidian Lissoclinum perforatum. There was a negative relationship between bioactivity and sponge growth forms, with encrusting species being more toxic, suggesting a trade-off in the allocation of energy for chemical defence purposes. Chemical bioactivity seemed to protect species from all studied phyla from inter-specific contact and toxic species generally lacked epibionts. Therefore, chemical bioactivity of benthic invertebrates has an important role in the structuring and functioning of marine cave communities, which deserves to be studied in the future.

6.3.2. Ecosystem engineering

Several marine cave-dwelling taxa have the ability to create, modify or destroy benthic habitats, thus having an important ecosystem engineering role. Sessile and sedentary benthic taxa can be assigned to different categories according to their ecosystem engineering activity (Gerovasileiou et al., 2017): (a) Habitat formers: providing habitat via their own living body; (b) Constructors: building structures with their mineral skeletons; (c) Binders: expanding and agglomerating the components of the habitat framework; and (d) Borers: penetrating actively in hard substrata via their bio-eroding activity.

Erect (arborescent/tree-like or tubular) and massive sponges, anthozoans, bryozoans and other sessile taxa create an upper layer which increases three-dimensional complexity of benthic communities (see 4.2.4 Volumetric stratification) and support assemblages of epibionts and associated macroinfauna. Navarro-Barranco et al. (2015) studied the species composition of amphipod assemblages associated to six taxa (i.e. the sponge Ircinia variabilis, the anthozoans Astroides calycularis and Parazoanthus axinellae, the polychaete Filograna implexa and the bryozoans Adeonella calveti and Pentapora fascialis) from Cerro Gordo Cave (Alboran Sea, Spain). In all host species, crustaceans (mostly amphipods) dominated in terms of abundance, but their assemblage structure differed significantly, with the scleractinian A. calycularis supporting the more distinctive assemblage.

In the oligotrophic Eastern Mediterranean Sea, erect anthozoans are absent or rare in marine caves, and thus, arborescent, massive and massive-tubular sponges, which often reach large sizes, create an upper layer in benthic communities (Gerovasileiou et al., 2015a, 2016a). The study of the macrofauna associated to the habitat-forming sponges Agelas oroides and Aplysina aerophoba in two marine caves of Lesvos Island (Aegean Sea, Greece), revealed a rich fauna consisting of 86 taxa (Gerovasileiou et al., 2016a). Crustaceans dominated in terms of abundance while polychaetes were the species-richest group. Although total species richness decreased from the entrance to inner dark cave sectors, mean density and diversity did not vary significant, suggesting that sponges maintain their functional role as "living hotels" across the caves by increasing habitat complexity in the impoverished inner dark cave sectors. Sponges, which represent one of the most abundant and species rich sessile group in Mediterranean marine caves (Gerovasileiou & Voultsiadou, 2012) exhibit a wide variety of ecosystem engineering activities in cave ecosystems (Gerovasileiou et al., 2017). In addition to the habitat-forming species, several others agglomerate

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[10] Even if algal filaments reach the inner semi-dark and dark sectors of marine caves, drifted by currents or waves, they fail to survive due to the partial or total lack of light (Moscatello & Belmonte, 2007).

carbonate particles, thus expanding the habitat framework (e.g. *Geodia* spp., *Spongia virgultosa*, *Faciospongia cavernosa* and various encrusting species) together with other invertebrate taxa (e.g. bryozoans) (Ballesteros, 2006; Gerovasileiou *et al.*, 2017). The category of borers includes several bio-eroding and insinuating sponges (e.g. *Cliona* spp.), which often form a considerable proportion of benthic biomass in marine caves, as well as the bivalves *Lithophaga lithophaga* and *Rocellaria dubia* (Corriero *et al.*, 2000; Ballesteros, 2006; Gerovasileiou *et al.*, 2017). Borers penetrate actively calcareous substrates, including biogenic ones, thus creating an endolithic layer (Riedl, 1966).

As described before, several invertebrate taxa contribute to the creation of bioconstructions with their hard body parts, skeletons or tubes, such as serpulid polychaetes, scleractinians, bryozoans, bivalves, and brachiopods (Gerovasileiou *et al.*, 2017). Foraminifers (e.g. *Miniacina miniacea* and *Rhizonubecula adherens*) and microbes also take part in the bioconstruction process (Sanfilippo *et al.*, 2015; Guido *et al.*, 2016a,b, 2017a,b). Typical bioconstructions include biostalactites, which are mainly formed by the serpulid *Protula tubularia* (Belmonte *et al.*, 2009; Sanfilippo *et al.*, 2015, 2017), and bryozoan nodules (Harmelin, 1985, 2000; Harmelin *et al.*, 2015; Rosso *et al.*, 2013b, 2015), which may develop in the transitional zone between the semi-dark and dark cave biocoenoses, and sometimes further inside the dark cave zones (see section sub-section 5.3.2). The size of the bioconstructions ranges from a few centimetres for bryozoan nodules up to nearly 1-m long for biostalactites.

Sponge-dominated community in an eastern Mediterranean cave.
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7. DYNAMICS & SEASONALITY

Early investigations on the successional dynamics of marine caves evidenced that the development of cave communities is an extremely slow process. Harmelin (1980) used limestone plates to investigate colonization of hard substrates under dark conditions in two marine caves of Marseille region (France): the blind-ended Trémies and the tunnel-shaped Moyade caves. While in the tunnel-shaped cave 9-10 years were sufficient for colonized plates to reach a mature state, with 100% of the substrate covered mainly by sponges and serpulids, in the blind-ended cave the biotic cover remained low and sponges were almost absent. These results suggest that marine caves are poorly resilient ecosystems.

The study of recruitment, settlement and primary succession of sessile benthos in the shallow, partly semi-submerged cave Grotta di Ciolo (Salento Peninsula, Italy), using baked clay panels, showed that while a 2-years recruitment period allowed for a complete colonization of panels at the entrance zone, recruitment process was very slow in the intermediate and inner dark zones, where mature benthic communities were not replicated on panels within the studied time frame (Denitto et al., 2007).

Temporal variability of marine cave communities, even on a short scale, has been rarely investigated. However, the study of sessile benthos in marine caves of Italy (Salento Peninsula) and Spain (Catalonia and Balearic Islands) showed that there are some seasonal differences in species number and cover, but they varied inconsistently with time and among caves (Martí et al., 2004a; Bussotti et al., 2006). The study of plankton assemblages along the horizontal axis of Grotta di Ciolo (Italy), revealed that the composition of the assemblage exhibited a clear seasonal cycle at the external and entrance zones of the cave, while the internal zone was differentiated, maintaining a restricted and less diverse pool of taxa throughout the year (Moscatello & Belmonte, 2007). The study of soft substrate meiofauna in the same cave (three sampling stations in the dark part of the cave, at 55, 75 and 90 m from the entrance) showed that there was a small seasonal variation in community structure (at the main group taxonomic level), and that the overall mean diversity did not vary with season, except for the station that was located closer to the entrance (Todaro et al., 2006). Russo et al. (2015) used artificial panels to study dynamics of hard substrate meiobenthos in the same cave, over a period of two years. As expected, taxa richness (at the family level) and the abundance of some taxa increased over time. Panel positioning seemed to affect the development of the assemblage only after

the first month of deployment. However, assemblage variability of the deployed artificial panels and on the natural substrate of the vertical cave walls was not explainable on the basis of seasonality.

A proper evaluation of ecosystem dynamics requires, as for every ecosystem, the availability of long-time series (Hampton et al., 2019), which are unfortunately rare in the Mediterranean Sea (Bianchi & Morri, 2004). The Ligurian Sea (NW Mediterranean) represents a partial exception, as historical data are available for a few marine caves. For instance, the sponge fauna of two semi-submerged caves was first studied in 1961-63 (Sarà, 1964) and again in 2015-16 (Nepote et al., 2016; Costa et al., 2018). The comparative analysis of these datasets revealed an increase in species richness and a significant change of growth forms, with massive sponges having been replaced by encrusting forms. Similar results had been obtained by Parravicini et al. (2010), who compared the sessile assemblages of the Grotta Marina of Bergeggi in 1986 and 2004, i.e. before and after the summer heat waves of 1999 and 2003. These positive thermal anomalies (with peaks up to 4°C above the climatological mean) were suggested to have selectively killed erect and massive organisms (such as the sponge Petrosia ficiformis), causing their replacement by encrusting taxa.

The Grotta Marina of Bergeggi is perhaps unique in the whole Mediterranean as it has been studied more or less regularly since the late 1970s (Bianchi et al., 1986; Sgorbini et al., 1988). The submerged part of the cave develops between sea surface and 7 m depth, has a relatively short length (about 40 m), but is remarkably tortuous and morphologically complex, with both tunnel-shaped and blind-ended portions, and exhibits paradigmatic gradients of light, water movement, sedimentation and – due to fresh water infiltration – of salinity. Cluster analysis on physical-chemical data[11] (Morri et al., 1994a) allowed recognizing four zones: (i) outer cave; (ii) main hall; (iii) shaft; and (iv) inner "lakes". Each zone had its own biological assemblage. The outer cave was inhabited by associations of sciaphilic algae but also by typical facies of the semi-dark biocoenosis (Laborel, 1960), characterized by sponges, large hydroids, and Parazoanthus axinellae. The main hall and the shaft harboured a typical biocoenosis of dark caves, with two different faunal zones (Laborel & Vacelet, 1959). In the biggest part of the main hall, massive sponges (e.g. Petrosia ficiformis) dominated. Scleractinians (e.g. Leptopsammia pruvoti and Polycyathus muellerae) were also abundant. The motile fauna included the mollusc Luria lurida and the crustaceans Dromia personata, Scyllarus arctus and

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[11] Water temperature (°C), salinity (psu), density (σ), water movement (cm·s⁻¹), light (µW·cm⁻²), pH, dissolved oxygen (ppm and % saturation), organic suspended matter (mg·l⁻¹ and % of total suspended matter), C/N ratio, chlorophyll-a (µg·l⁻¹), sediment mean grain size (mm), and % of fine (<0.25 mm) sediments.

Hemimysis speluncula, the latter forming huge swarms. In the shaft, sponges were less abundant (but included *Petrobiona massiliana*). Serpulids (*Protula tubularia*, *Serpula cavernicola* and *Spirorbis cuneatus*) and brachiopods (*Argyrotheca cuneata*) were the most important elements of the sessile fauna. Motile fauna included the crustaceans *Herbstia condyliata*, *Lysmata seticaudata* and *Stenopus spinosus* and the fishes *Apogon imberbis*, *Grammomus ater*, *Sciaena umbra* and *Thorogobius ephippiatus*. Finally, the inner lakes, with still water where pH fell to 7.8 and salinity to 21.2 due to freshwater infiltrations, harboured an extremely poor and rarefied assemblages, mostly characterized by scattered serpulids (*Spirobranchus polytrema*).

The above situation remained apparently stable for about two decades. However, increased sea water temperature since the 1990s induced the substitution of the cold-water species *H. speluncola* by the warm-water congener *Hemimysis margalefi* (Chevaldonné & Lejeusne, 2003). Such a species shift is likely to exert great influence on the energy budget of cave ecosystems (Bianchi, 2007). Mysids stay in caves during the day but move outside at night to feed (see chapter 6). In so doing, they import organic matter from outside into the oligotrophic cave ecosystem, but *H. speluncola* typically forms huge swarms while *H. margalefi* small groups. Modifications in the sessile assemblages led to a general homogenisation of the cave communities, and the four biotic zones characterizing the cave were less sharply distinguishable.

Thanks to the availability of a 30-year-long series of quantitative data (substratum cover from wire-frame photographs) on the sessile communities of the Grotta Marina of Bergeggi, Montefalcone *et al.* (2018) evaluated ecosystem change using non-taxonomic descriptors, namely growth forms and trophic guilds, which provide information about ecosystem structure and functioning, respectively. The cave experienced a general trend of change during the last three decades, mainly due to the decline in the cover of sessile organisms (especially three-dimensional forms). The most important rate of change was observed between 2009 and 2013, coinciding with recent major local disturbances

deriving from coastal interventions. Structural aspects, but not functional ones, have been showing some recovery in recent years. Similar results were obtained from two caves at Ventimiglia (Italy), regularly monitored between 2010 and 2015 to assess the impact of the construction of a tourist harbour (Nepote *et al.*, 2017).

Important temporal changes have been also documented from marine caves of Spain. The comparison of photographic material collected in 1978 and 2016 from the ceiling and bottom of the submerged tunnel-shape cave Túnel del Dofí, a popular SCUBA diving spots in Medes Islands (Catalonia), revealed significant changes in benthic community structure (composition and abundance). More specifically, three-dimensional growth forms (e.g. the red coral *C. rubrum* and the bryozoans *Scrupocellaria* sp. and *Reteporella grimaldii*) decreased in abundance, with a parallel increase of encrusting sponges and air-chambers on the ceilings (from 0.7% in 1978 to 9.07% in 2016), caused by the air bubbles exhaled from divers (Burgués *et al.*, 2016).

More recently, the study of sessile benthos in Cerro-Gordo submerged cave (Granada, Spain), over a decade (2007 to 2016), using taxonomic and morphological descriptors (i.e. major taxonomic groups and growth forms, respectively), revealed significant temporal variability in community structure and morphology in both external and internal cave sectors (Sempere-Valverde *et al.*, 2019). During the examined timeframe, sponge cover decreased, while that of polychaetes and brachiopods increased, especially in the inner dark sector. In the semi-dark cave sector, domed morphologies also decreased through time.

The absence of long-time series depicting the past ecological state of the marine cave habitat in several Mediterranean regions (e.g., Eastern and South-ern sub-areas) is a major impediment to monitoring and evaluating of potential impacts and changes in their ecological status (Gerovasileiou *et al.*, 2016c; SPA/RAC-UN Environment/MAP & OCEANA, 2017, Sempere-Valverde *et al.*, 2019).

Dark cave biocoenosis dominated by serpulids and sponges (e.g. *Plakina* spp.).
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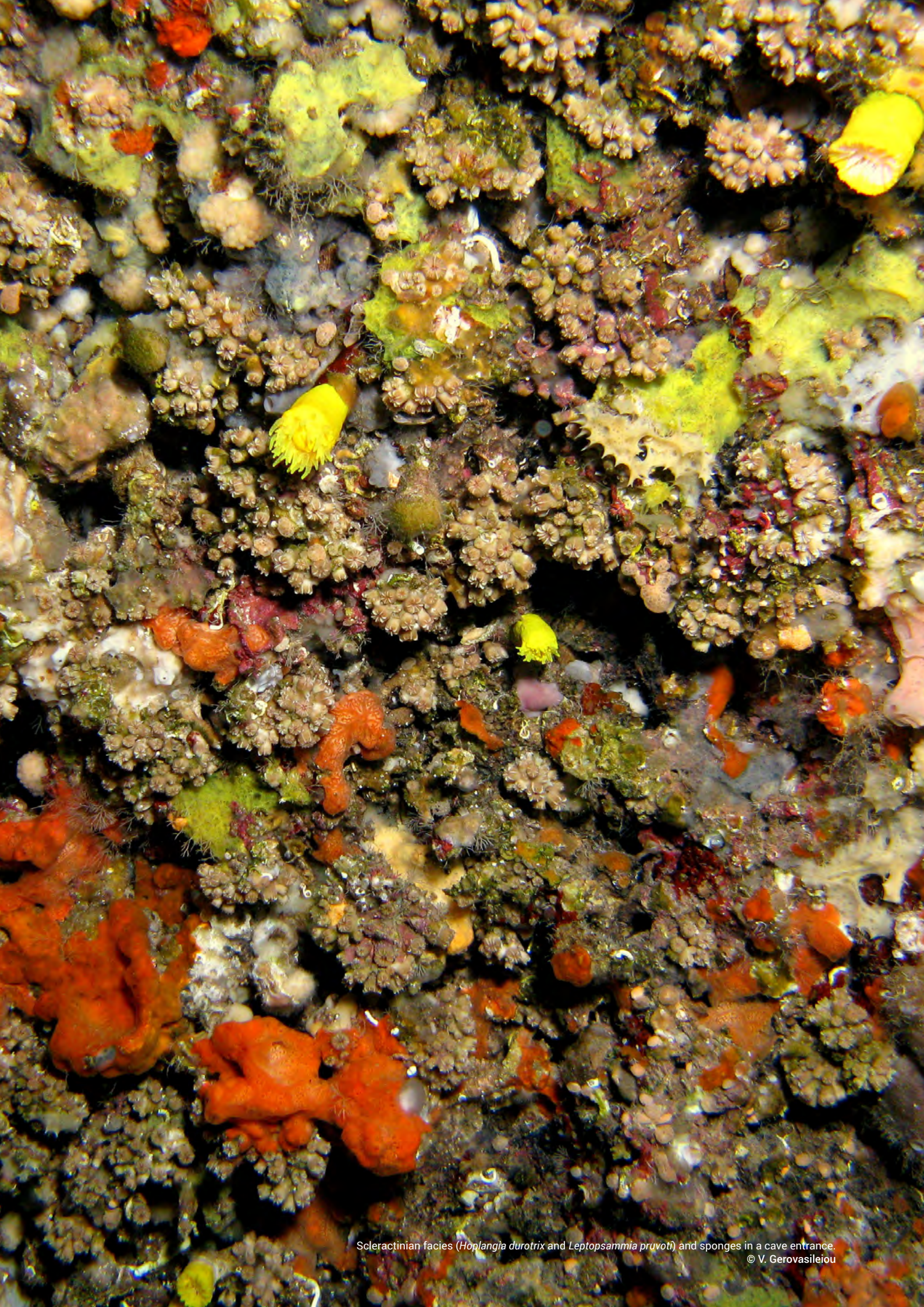
Scleractinian facies (*Hoplangia durotrix* and *Leptopsammia pruvoti*) and sponges in a cave entrance.
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8. BIODIVERSITY

From the first pioneer biological studies in Mediterranean marine caves it became evident that they harbour rich benthic communities and several previously undescribed species (see chapters 3 and 4). The historical monograph "Biologie der Meereshöhlen" by the Austrian zoologist Rupert Riedl (1966), which provided a first synthesis of existing knowledge, listed a total of 905 taxa from Mediterranean marine caves, estimating that the overall diversity could reach 2000 species. Many of these taxa (529 taxa belonging to 32 major groups) were recorded during the "Tyrrhenia-Expedition", which focused mostly on marine caves of the Tyrrhenian Sea. Some decades later, a monograph on the existing information on marine caves of Italy, including chapters on different taxonomic groups, was published by Cicogna *et al.* (2003). More recently, a number of reviews, meta-analyses, checklists, and large-scale surveys on marine cave biota were published for particular taxa, such as sponges (e.g. Gerovasileiou & Voultsiadou, 2012; Manconi *et al.*, 2013; Grenier *et al.*, 2018) and fishes (Bussotti *et al.*, 2015), for the entire Mediterranean (Gerovasileiou & Voultsiadou, 2014) or particular regions (Gerovasileiou *et al.*, 2015a). The latter study, combined information from 62 literature sources with data from primary research in 23 marine caves, focusing on the Eastern Mediterranean Sea, and listed 520 taxa which belonged to 34 groups.

8.1. Overall diversity and regional patterns

The overview of 312 literature sources (peer-reviewed and grey literature) showed that 2267 taxa belonging to 58 taxonomic groups were reported from ≈350 marine caves (mostly semi-submerged and/or shallow) in 15 Mediterranean countries. However, as expected, not all Mediterranean areas and taxonomic groups have received the same effort. The majority of the caves studied (93%) were located in the Northern Mediterranean coasts, with Italy, France, and Spain being the main countries where marine cave research has taken place (121, 86 and 52 studies, respectively). As explained before (see chapter 3), these are the main countries where marine cave biological research started in the Mediterranean Sea. Sponges were by far the most well-studied group (160 studies), followed by anthozoans (87), polychaetes (63), bryozoans (60), decapods (42), bivalves (42) and fishes (40) (Table 8.1). Very few studies examined microbes, planktonic taxa and miscellaneous "small" groups, such as soft substrate meio- and macrofauna. The number of species per taxonomic group and marine area were positively correlated to research effort, expressed as the number of studies and caves explored (Gerovasileiou & Voultsiadou, 2012; 2014). Research in a greater number of marine caves in different Mediterranean areas is expected to lead to an increment in the number of known species, particularly within "inconspicuous" groups (Bianchi, 2007).

Table 8.1 Number of studies and marine caves by Mediterranean area and taxonomic group. The proportion of number of taxa in marine caves against the total Mediterranean diversity for each taxonomic group was calculated based on data in Coll *et al.* (2010), Rosso & Di Martino (2016). AL, Alboran Sea; CC, Catalan coast; BS, Balearic Sea; SS, Sardinian Sea; FC, French Coast; LS, Ligurian Sea; TS, Tyrrhenian Sea; TC, Siculo-Tunisian Strait; AN, North Adriatic; AS, South Adriatic; IS, Ionian Sea; NA, North Aegean; SA, South Aegean; LB, Levantine Basin; CE, Cave entrance zone; SD, Semi-dark cave zone; D, Dark cave zone. Updated from Gerovasileiou & Voultsiadou (2014) and Gerovasileiou (2014) with recent data for Foraminifera, Porifera, Bryozoa, Echinodermata, Tunicata and Pisces.

Taxonomic group	Mediterranean areas														Cave zone			Number of studies	Number of taxa	Proportion of Mediterranean diversity (%)
	AL	CC	BS	FC	LS	SS	TS	TC	AN	AS	IS	NA	SA	LB	CE	SD	D			
Bacteria							+		+							1	10	7	12	-
Bacillariophyceae							+										5	1	5	0.7
Foraminifera		+	+	+		+	+					+	+		7	8	10	18	90	15
Myzozoa											+					1	1	1	1	-
Ciliophora											+				11	16	15	2	20	-
Radiozoa											+				2	2	2	1	2	-
Phaeophyceae		+	+	+	+	+	+	+	+	+	+	+	+		33	2		19	33	12.2
Chlorophyta		+	+	+	+	+	+	+	+	+	+	+	+		27	4		24	27	14.2
Rhodophyta		+	+	+	+	+	+	+	+	+	+	+	+	+	169	30		31	169	25.7
Porifera	+	+	+	+	+	+	+	+	+	+	+	+	+	+	137	213	189	160	329	48
Hydrozoa		+	+	+	+	+	+	+	+		+	+	+	+	49	60	17	33	108	23.6
Scyphozoa			+									+			2	2	1	2	4	20
Anthozoa	+	+	+	+	+	+	+	+	+	+	+	+	+	+	24	26	25	87	49	29.7
Ctenophora					+							+				1		3	1	3.3
Platyhelminthes							+		+			+			3	4	3	2	36	4
Nemertea							+		+		+				3	3	3	2	9	5.2
Nematoda																		3	37	5.3
Rotifera																		1	2	3.4
Kinorhyncha							+		+									1	1	3.6
Priapulida										+	+						1	1	1	20
Gastrotricha											+						16	2	16	9.7
Entoprocta				+					+								2	4	4	21.1
Copepoda			+			+			+		+				49	38	53	17	113	28
Ostracoda				+			+								1	1	2	4	8	1.6
Cirripedia		+		+	+			+	+		+				1	1	4	13	7	17.5
Decapoda		+	+	+	+	+	+	+	+		+	+	+	+	23	43	34	42	73	19,1
Mysida		+	+	+	+	+	+	+	+	+	+		+		6	6	7	22	21	20,6

Taxonomic group	Mediterranean areas														Cave zone			Number of studies	Number of taxa	Proportion of Mediterranean diversity (%)
	AL	CC	BS	FC	LS	SS	TS	TC	AN	AS	IS	NA	SA	LB	CE	SD	D			
Thermosbaenacea			+														1	1	1	20
Facetotecta											+							1	1	-
Tanaidacea	+			+			+		+			+				3	4	6	6	14
Pentastomida	+										+						1	1	1	-
Isopoda	+			+			+		+		+	+			2	7	6	11	15	9,1
Leptostraca			+														1	2	1	16,7
Amphipoda	+	+	+	+	+		+								26	59	30	18	83	18.5
Cumacea	+			+			+									2	5	6	6	6.1
Branchiopoda											+				3	4	3	1	4	-
Pycnogonida				+			+								1	3	1	3	9	20
Acari							+											2	5	-
Insecta (marine)											+				1	1		1	1	0.4
Oligochaeta							+											4	2	-
Polychaeta	+	+	+	+	+	+	+	+	+		+	+	+	+	86	186	113	63	262	23.3
Sipuncula				+			+		+			+			2	5	3	9	6	16.7
Echiura			+		+				+			+			1		1	3	1	16.7
Polyplacophora				+			+								5			7	7	22.6
Gastropoda		+	+	+	+	+	+	+	+		+	+	+	+	68	76	39	37	134	8.6
Bivalvia		+	+	+	+	+	+	+	+		+	+		+	31	41	29	42	90	22.5
Caudofoveata							+									1		1	1	3.4
Cephalopoda					+				+			+			3	2		3	3	4.6
Tardigrada				+			+			+	+						1	3	31	40.3
Bryozoa	+	+	+	+	+	+	+	+	+		+	+	+	+	121	168	132	60	228	41
Brachiopoda	+	+	+	+	+	+		+	+	+	+	+	+	+		7	8	20	9	64.3
Phoronida												+			1	1		1	1	20
Chaetognatha				+		+					+				1	1	5	3	5	25
Pterobranchia				+													1	1	1	20
Echinodermata	+	+	+	+	+		+	+	+		+	+	+	+	17	21	17	29	35	22.7
Tunicata		+	+	+		+	+	+	+		+	+	+	+	24	24	13	34	44	19.2
Pisces		+	+	+	+	+	+	+	+	+	+	+	+	+	45	46	29	40	96	14.8
Mammalia	+										+	+	+	+	1	1	1		1	4.3
Number of studies	12	15	31	87	21	12	67	17	28	15	40	24	16	27				312		
Number of caves	12	4	31	47	25	16	58	18	27	27	41	11	36	17						
Number of taxa	70	287	408	670	141	252	897	180	383	154	711	314	161	178	985	1120	844		2267	13.3%

Most taxa were reported from the semi-dark zone of marine caves (1120), followed by the entrance (985) and the dark zone (844) while for 510 taxa the zone was not specified in the literature sources[13] (Table 8.1). Macroalgae (mostly rhodophytes) dominated in terms of species richness in the entrance zone (23% of the species) while sponges dominated in the semi-dark and dark zones (19% and 22.4%, respectively). Bryozoans and polychaetes were also among the richest groups in all zones. A total of 332 taxa were recorded in sediments of the cave bottom and 53 taxa in anchialine/marginal caves [14].

8.2. Marine cave biota

This section aims to provide an outline of existing knowledge (diversity patterns, frequently recorded taxa[15], etc.) on Mediterranean marine cave biodiversity for the main taxonomic groups (Table 8.1).

• Prokaryotes

The microbial diversity of Mediterranean marine caves has been very little studied, thus not allowing for the description of general diversity patterns. Most available studies concern microbial mats of the famous Grotta Azzurra and Grotta Sulfurea in Italy (e.g. Mattison *et al.*, 1998; Canganella *et al.*, 2002; 2007), and more recently, marine caves and cavities of Zakynthos Island, Greece (Polymenakou *et al.*, 2018) (see sub-section 6.1.3.3). Microbial mats have been also reported from organic-rich sediments that accumulate in shallow marine caves at Ventimiglia (Italy), following disturbances (Nepote *et al.*, 2017) and in a shallow cave of the North Aegean Sea (Daskalaki *et al.*, 2018).

• Macroalgae

Macroalgae can be very abundant at the entrance zone of marine caves and, in some cases, sciaphilic species penetrate further inside semi-dark cave sectors, though with minor cover (Riedl, 1966; Cinelli *et al.*, 1977; Bianchi, 2003; Alongi *et al.*, 2012; Gerovasileiou *et al.*, 2017). A considerable number of macroalgae taxa have been reported from Mediterranean marine caves, specifically 27 Chlorophyta, 33 Phaeophyceae and 169 Rhodophyta. The most frequently reported species (all in >10 caves) were the chlorophytes *Palmophyllum crassum, Flabellia petiolata, Halimeda tuna, Valonia macrophysa*; the phaeophytes *Halopteris filicina* and *Dictyota dichotoma*; and the rhodophytes *Peyssonnelia squamaria, Lithophyllum stictiforme, Peyssonnelia rubra, Plocamium cartilagineum*, and *Sphaerococcus coronopifolius*.

• Foraminifers

The most widely reported foraminifer in Mediterranean marine caves is *Miniacina miniacea* (in >20 caves), which is a sessile benthic species, clearly visible to the naked eye. It can cover up to 1% of the total biotic cover on hard substrates inside marine caves (Dimarchopoulou *et al.*, 2018), and together with other taxa, it contributes to the formation of bioconstructions (Ballesteros, 2006; Sanfilippo *et al.*, 2015; see sub-section 6.3.2). Very few studies provide scattered information about benthic (e.g. Riedl, 1966; Rosso *et al.*, 2019) or planktonic foraminifers (e.g. Moscatello & Belmonte 2007), in most cases identified at higher taxonomic levels (e.g. family, order). In the latest census on Mediterranean marine cave biodiversity, a total of 14 foraminifer taxa were reported. However, a recent study in the Bel Torrente Cave of Sardinia (Italy) by Romano *et al.* (2018), yielded 106 foraminifer species in cave sediments, of which 76 were represented both by dead and living specimens. Therefore, the known foraminifer diversity of Mediterranean marine caves should be approximately 90 taxa (considering only living species).

• Sponges

Porifera is one of the most abundant and species rich phylum in Mediterranean marine caves (Sarà, 1962b; Pouliquen, 1972; Corriero *et al.*, 2000; Gerovasileiou & Voultsiadou, 2012, 2016; Manconi *et al.*, 2013; Grenier *et al.*, 2018). A total of 329 sponge species from all classes (279 Demospongiae, 29 Calcarea, 20 Homoscleromorpha, and 1 Hexactinellida), which constitute 48% of the Mediterranean sponge diversity, have been recorded from at least 185 marine caves (Gerovasileiou & Voultsiadou, 2012 and unpublished data). Certain taxa seem to be highly represented in the marine cave habitat, such as homoscleromorphs (e.g. *Oscarella* spp. and *Plakina* spp.), dictyoceratids and lithistids. A high proportion of the marine cave sponges are Mediterranean endemics (41%), including rare species with narrow distribution range, relict species (e.g. *Petrobiona massiliana*), living fossils (e.g. lithistids) and >30 cave-exclusives (Gerovasileiou & Voultsiadou, 2012; Grenier *et al.*, 2018; Lage *et al.*, 2018; 2019). In addition, several deep-sea species were found in dark marine caves, such as the carnivorous cladhorizid Lycopodina hypogea and the hexactinellid *Oopsacas minuta* (Vacelet *et al.*, 1994; Vacelet & Boury-Esnault, 1995). The most frequently recorded sponges (in >30 caves) in Mediterranean caves are the demosponges *Agelas oroides, Petrosia ficiformis, Spirastrella cunctatrix, Ircinia variabilis, Phorbas*

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[13] Therefore, empty cells for cave zones in Table 8.1 do not necessarily indicate absence.
[14] Only the marine and brackish-water layers were considered in the study.
[15] Species reported from a considerable number of marine caves, at the Mediterranean scale, according to data from the Mediterranean marine cave biodiversity database by Gerovasileiou & Voultsiadou (2012, 2014). Order of species within each taxonomic group is presented in a decreasing number of records. Each record represents occurrence in a different Mediterranean marine cave. All cave zones, from the entrance to the inner dark zone, were considered.

tenacior, Crambe crambe, Chondrosia reniformis, Axinella damicornis, Spongia virgultosa, Acanthella acuta, Penares euastrum, Terpios gelatinosa, Aaptos aaptos, Diplastrella bistellata, Haliclona mucosa, Erylus discophorus, Aplysilla rosea, Haliclona sarai, Ircinia oros, Cliona viridis, Penares helleri, and *Spongia officinalis*; the calcareous sponges *Clathrina coriacea* and *P. massiliana*; and the homoscleromorph *Oscarella lobularis*. Due to the lack of light and space-competing algae, sponges, which are generally sciaphilic animals, turn marine caves into a real "sponge realm", with a maximum of 86 taxa recorded within a single cave (Grotte du Figuier, Marseille). Nevertheless, most species (67%) are known from only 1-5 caves, with 34.5% reported from a single cave, thus indicating the fragmentation and individuality of the cave habitat (Gerovasileiou & Voultsiadou, 2012).

• **Cnidarians**

A total of 161 cnidarian species have been reported from Mediterranean marine caves (49 Anthozoa, 108 Hydrozoa and 4 Scyphozoa). Anthozoans represent the most abundant and widespread taxon in marine caves, where they can form dense facies, especially on the ceilings and walls of the semi-dark cave zone, such as (a) the scleractinians *Leptopsammia pruvoti, Madracis pharensis* (very abundant in the Eastern Mediterranean), *Hoplangia durotrix, Polycyathus muellerae, Caryophyllia inornata* and *Astroides calycularis* (mostly in South-Western Mediterranean), some of which can be also abundant in darker sectors, (b) the red coral *Corallium rubrum*, which is more common in the North-Western Mediterranean; and (c) *Parazoanthus axinellae*, which can be abundant in cave entrances or in semi-dark tunnels with high hydrodynamics (Pérès, 1967; Zibrowius, 1978; Gili & Ballesteros, 1991; Gerovasileiou *et al.*, 2015a; see sub-section 5.3.1). In addition, gorgonian facies (e.g. *Eunicella cavolini* and *Paramuricea clavata*) can develop at cave entrances, mostly in the Western Mediterranean (see sub-section 4.2.4). The most common anemone in marine caves, *Cerianthus membranaceus*, is often found on the sediment of cave bottoms, in both semi-dark and dark zones. Hydroids prefer cave sectors with good water circulation, such as entrances or tunnels (e.g. Riedl, 1966; Balduzzi *et al.*, 1989; Bianchi & Morri, 1994; Morri *et al.*, 2009). The most frequently recorded hydroid species in Mediterranean marine caves are *Clytia linearis* (Lessepsian migrant), *Campanularia hincksii, Clytia hemisphaerica, Obelia dichotoma, Eudendrium racemosum* and *Antennella secundaria* (all recorded in >10 caves). Interestingly, 8 non-indigenous hydroids have been reported in caves (Gerovasileiou *et al.*, 2016c), mostly in the Levantine Sea (Morri *et al.*, 2009), with the circumtropical *C. linearis* being the most widespread throughout the Mediterranean.

• **Annelids**

A high number of polychaete species (262) were recorded in Mediterranean marine caves, mostly on hard substrates. The most frequently reported species belong to the families Serpulidae (e.g. *Protula tubularia, Serpula vermicularis, Semivermilia crenata, Filogranula annulata, Spiraserpula massiliensis, Vermiliopsis labiata, Josephella marenzelleri, Filograna implexa*) and Syllidae (e.g. *Trypanosyllis zebra, Syllis hyalina, Haplosyllis spongicola, Syllis variegata*), which thrive on hard substrates (all recorded in >10 caves). Although none of these species are cave-exclusives (Belloni & Bianchi, 1982), some serpulids can be considered typical of the cave habitat, such as *Serpula cavernicola, Spiraserpula massiliensis* and *Vermiliopsis monodiscus* (Zibrowius, 1968; Fassari & Mòllica, 1991; Bianchi & Sanfilippo, 2003; Sanfilippo *et al.*, 2017). The rest of the serpulids found in marine caves have been assigned to four main ecological groups: sciaphilic/coralligenous taxa, deep-water taxa, shallow-shelf taxa and shelf taxa (Rosso *et al.*, 2013b; Sanfilippo *et al.*, 2017). Serpulids are usually the most abundant taxon, in terms of cover, in the dark cave biocoenosis, where some species tend to aggregate and form bioconstructions (see sub-section 5.3.2). Approximately 60 polychaete taxa have been reported from cave sediments, with the most frequently reported species being *Chrysopetalum debile* and *Sabella spallanzanii* (in >5 caves). Some other species were found to be abundant in particular caves (e.g. *Levinsenia gracilis* in Grotta Azzurra of Capo Palinuro, Italy; see sub-section 5.4.1). However, the small number of studies focusing on soft substrate macrobenthos does not allow for the generalization of diversity patterns.

• **Miscellaneous "small" taxa**

A wide variety of small-sized planktonic, macro- and meiobenthic taxonomic groups (for crustaceans see below) are represented in Mediterranean marine caves (Table 8.1). Due to the scarcity of studies on soft substrate macro- and meiofauna and zooplankton assemblages (see sub-sections 5.4.1 and 5.4.2), there is little information about their diversity in this particular habitat. However, 40% of the Mediterranean tardigrade fauna has been reported from marine caves of Italy (e.g. de Zio Grimaldi & Gallo D'Addabbo 2001), while many new species belonging to "small" invertebrate groups were found in soft sediments of marine caves of Italy and France (Casanova, 1986; Villora-Moreno, 1996; Fregni *et al.*, 1998; Gallo D'Addabbo *et al.*, 2001; Todaro & Shirley, 2003). Although these species have not been found in other habitats so far, it is not sure whether they are cave-exclusives or deep-sea species (Zeppilli *et al.*, 2018). These include the priapulid *Tubiluchus troglodytes*, the gastrotrich *Urodasys acanthostylis*, the tardigrades *Parastygarctus mediterranicus, Pseudostygarctus rugosus* and *Trogloarctus trionyches*, and the chaetognath *Spadella ledoyeri*.

• Arthropods

A total of 355 arthropods from several taxonomic groups, mostly crustaceans, have been reported so far from Mediterranean marine and anchialine caves (Table 8.1). The groups with the highest number of species were Copepoda (113), Amphipoda (83), Decapoda (73), Mysida (21) and Isopoda (15), with all other groups comprising less than 10 taxa. The most frequently reported species (in >10 caves) were the decapods *Stenopus spinosus, Herbstia condyliata, Palinurus elephas, Palaemon serratus, Dromia personata, Galathea strigosa, Plesionika narval* and *Scyllarus arctus*, and the mysids *Hemimysis margalefi, Hemimysis speluncola* and *Siriella jaltensis*. These species move outside-inside caves, with the first two mysids forming swarms, thus playing an important role in the functioning of the marine cave ecosystem (see sub-sections 6.1.3 and 6.2). The high number of copepod species in Mediterranean caves was basically sourced from one study on zooplankton assemblages of Grotta di Ciolo, Italy (Moscatello & Belmonte, 2007) and one study on soft substrate meiobenthos of 3PP Cave, France (Janssen *et al.*, 2013). Nevertheless, both studies listed a considerable number of taxa which were either undetermined or identified only at higher taxonomic levels, which were not considered in the census by Gerovasileiou & Voultsiadou (2014). Interestingly, 75% of the taxa found by Janssen *et al.* (2013) were undescribed and several had deep-sea affinities. In addition, many new copepods, decapods and a thermosbaenacean species, probably all cave-exclusive, were found from marine and anchialine caves of the Adriatic Sea and the Balearic Islands (e.g. Pretus, 1990; Fransen, 1991; Jaume & Boxshall, 1996; Jaume, 1997; Jaume *et al.*, 1999). More recently, the molecular study of mysids in several marine caves from different Mediterranean areas by Rastorgueff *et al.* (2014) revealed that at least four undescribed cryptic *Hemimysis* taxa occur. The above results indicate that further studies on planktonic, hyperbenthic and meiobenthic fauna in marine and anchialine caves would shed light on new crustacean diversity.

• Molluscs

Several studies showed that Mediterranean marine caves harbour a rich malacofauna, and especially (micro-)gastropods (e.g. Starmühlner, 1968; True, 1970; Cantone *et al.*, 1979; Cattaneo, 1981, 1982; Cattaneo-Vietti & Russo, 1987). Molluscs are represented in Mediterranean caves by 235 species, mostly gastropods (134) and bivalves (90). Other classes are represented with less than 10 species (7 Polyplacophora, 3 Cephalopoda and 1 Caudofoveata). The most frequently reported species are the nudibranch *Peltodoris atromaculata*, which grazes on the cyanobacteria of the sponge *Petrosia ficiformis*, the bio-eroding bivalves *Lithophaga lithophaga* and *Rocellaria dubia* (see sub-section 6.3.2) and the spiny file clam *Lima lima* (all in >10 caves). The protected

gastropods *Erosaria spurca* and *Luria lurida* are more commonly observed in caves than elsewhere (Bianchi, 2003). The gastropod *Homalopoma sanguineum* was observed to reach unusually high abundance in the Y-Cave of Croatia (Radolović *et al.*, 2015). Only one mollusc species has been reported exclusively, so far, from marine caves, namely the gastropod *Hyalogyra zibrowii*, that was recorded in the muddy bottom, rich in *Posidonia* detritus, of the dark sector of Bagaud Cave (South France), at 7 m depth and 10 m from the entrance (Warén *et al.*, 1997). A total of 15 non-indigenous molluscs (8 bivalves and 7 gastropods) have been recorded in Mediterranean marine caves, mostly of Lebanon, such as *Brachidontes pharaonis, Spondylus spinosus* and *Chama pacifica* which seem to have replaced native habitat-forming bivalves that were present in the past (Crocetta *et al.* 2013a,b; Crocetta & Russo 2013; Gerovasileiou *et al.*, 2016c).

• Brachiopods

Brachiopoda exhibit a particular preference for marine caves, often developing in large populations on the ceiling of the dark sectors (Logan *et al.*, 2004). Out of the 13-14 brachiopods occurring in the Mediterranean Sea, 9-10 (64-70%) have been found in marine caves. The most frequently recorded species are *Joania cordata, Argyrotheca cuneata, Novocrania anomala* (also including records of the doubtful species *N. turbinata*), *Argyrotheca cistellula, Tethyrhynchia mediterranea*, and *Megathiris detruncata*. The rhynchonellid *T. mediterranea* was first recorded and described from marine caves of South France and Tunisia (Logan & Zibrowius, 1994) and has not been found from other habitats to date. The species *N. anomala* can be found in considerable numbers, cemented on dark cave walls and ceilings, also contributing to the formation of bioconstructions (Logan *et al.*, 2004; Radolović *et al.*, 2015; Rosso *et al.*, 2019; see sub-section 5.3.2). Several brachiopods can be found in sediments of the cave bottom as thanatocoenoses, having detached from the cave ceiling (Taddei Ruggiero, 1994).

• Bryozoans

Bryozoans are among the dominant phyla in Mediterranean marine caves, in terms of both cover and species richness (Harmelin, 1985, 1986, 2000; Rosso *et al.*, 2019). In the Mediterranean Sea, marine caves are the single habitat richest in bryozoans, hosting 228 species (Gerovasileiou & Voultsiadou, 2014; Rosso & Di Martino, 2016; Rosso *et al.*, 2019). Most species are cheilostomes (181), followed by cyclostomes (37) and ctenostomes (10). Despite their small number, ctenostomes are represented with a slightly higher species percentage in marine caves compared to other habitat types (4.5 versus <2%), possibly due to the availability of special microenvironments offered by some sponges (Rosso & Di Martino, 2016). Within caves, the highest bryozoan cover has been observed in the transitional zone between the semi-dark and

dark cave biocoenosis, where several encrusting taxa form nodular and crest-like bioconstructions, and thus create a vertical microstratification (Harmelin, 1985, 2000, 2003; Harmelin *et al.*, 1985; Rosso *et al.*, 2013b, 2015, 2019; see sub-sections 5.3.2 and 6.3.2). The most frequently reported species in Mediterranean marine caves (>10 caves) are the cheilostomes *Myriapora truncata, Celleporina caminata, Crassimarginatella maderensis, Aetea truncata, Cribrilaria radiata, Escharina vulgaris, Reteporella grimaldii, Chlidonia pyriformis, Caberea boryi, Cribrilaria innominata, Glabrilaria pedunculata, Fenestrulina malusii, Adeonella calveti, Escharoides coccinea, Margaretta cereoides, Reptadeonella violacea, Schizotheca fissa, Schizoretepora serratimargo*; and the cyclostomes *Crisia sigmoidea, Disporella hispida, Diplosolen obelius, Harmelinopora indistincta, Annectocyma major* and *Crisia pyrula*. Several bryozoan species were first found and described from Mediterranean marine caves (e.g. Hayward, 1974; Silén & Harmelin, 1976; Harmelin *et al.*, 2007; Rosso *et al.*, 2019). According to Harmelin (1986) the bryozoan fauna of dark caves presents affinities with that of other crevicular micro-habitats (e.g. coralligenous concretions), undersides of small hard substrates, and deep-sea habitats. Rosso *et al.* (2013b) distinguished five ecological categories of bryozoans in marine caves of Sicily: cave species, sciaphilic and/or coralligenous taxa, deep-water taxa, shallow-shelf taxa and shelf taxa. Recent studies in marine caves of Lebanon revealed the presence of non-indigenous taxa and new species with Indo-Pacific affinities (Harmelin *et al.*, 2007, 2009, 2014a,b).

• Echinoderms

The echinoderm fauna of Mediterranean marine caves is represented by 35 species in total. The most frequently reported taxa (>10 caves) are the sea urchin *Arbacia lixula*, which can occasionally enter in shallow caves, and the brittle star *Ophiothrix fragilis*. Echinoderms are rarely abundant in caves except for some ophiurids (e.g. *Amphiura chiajei*; see sub-section 5.4.1). The crinoid *Antedon mediterranea* is abundant in the Grotta Azzurra of Capo Palinuro, Italy (Bianchi *et al.*, 1994; Cinelli *et al.*, 1994). The same species and the sea urchin *Stylocidaris affinis* have been also observed in some marine caves of Crete, Greece (V. Gerovasileiou, personal observations).

• Tunicates

A total of 44 tunicate species have been recorded in Mediterranean marine caves, mostly Ascidiacea, except for two undetermined salps drifted from outside (Moscatello & Belmonte 2007). The most frequently reported ascidians are *Halocynthia papillosa* (18 caves) and *Microcosmus vulgaris* (7). *Pyura vittata* was also mentioned as a typical species of the semi-dark cave biocoenosis by Pérès (1967). The rare species *Rhodosoma callense*, which has the shape of a

box with an articulated lid, was found and re-described again, for the first time after its first description in the 19th century, in two marine caves of Marseille (France) by Monniot & Zibrowius (1999). Some non-indigenous species (e.g. *Herdmania momus, Phallusia nigra* and *Symplegma brakenhielmi*) have been recorded in Eastern Mediterranean caves (Gewing *et al.* 2014; Gerovasileiou *et al.*, 2016c; see Box 2.1). Ascidians are rarely abundant in caves, although some colonial species (e.g. *Clavelina* spp.) can locally form patches (Bianchi, 2003).

• Fish

Mediterranean marine caves are used as shelters by several fishes (Riedl, 1966; Bussotti *et al.*, 2002, 2003, 2015, 2017; Bussotti & Guidetti, 2009; Gerovasileiou & Voutlsiadou, 2014; Gerovasileiou *et al.*, 2015a,b). Approximately 100 fish species have been reported from different sectors of Mediterranean marine caves, including sporadic visitors. According to Bussotti *et al.* (2015, 2017) fishes in marine caves can be assigned to three main ecological categories: (1) species typically inhabiting marine caves, such as *Gammogobius steinitzi, Grammonus ater* and *Didogobius splechtnai*; (2) species associated to cryptic habitats (e.g. crevices and fissures), also frequently found in caves, such as *Apogon imberbis, Conger conger, Corcyrogobius liechtensteini, Epinephelus marginatus, Scorpaena maderensis* (more common in the Eastern Mediterranean), *S. notata, S. porcus, Sciaena umbra, Serranus cabrilla, S. scriba, Phycis phycis,* and *Thorogobius ephippiatus*; and (3) several nectobenthic species inhabiting rocky reefs that can be occasionally found in caves, but usually close to the entrance (e.g. *Coris julis, Diplodus* spp., *Sarpa salpa* and *Symphodus* spp.). The cardinal fish *A. imberbis* is by far the most frequently reported and abundant species in marine caves, contributing to the mitigation of trophic depletion through its nychthemeral migrations inside-outside (see sub-section 6.1.3.1). Among the most recent additions to the Mediterranean cave fish fauna, are the deep-water Messina rockfish *Scorpaenodes arenai* that was photographed for the first time with scuba in a submerged cave (26-31 m) of Zakynthos Island, in Greece (Gerovasileiou & Bailly in Tsiamis *et al.*, 2015), and non-indigenous species of Indo-Pacific origin (e.g. *Sargocentron rubrum* and *Pempheris rhomboideia*) in caves of the Eastern Mediterranean Sea (Gerovasileiou *et al.*, 2016c).

• Birds and Mammals

Some seabirds that inhabit the rocky coasts often find refuge, especially at the time of nesting, in the sub-aerial part of large semi-submerged caves. The Mediterranean monk seal *Monachus monachus* is one of the most emblematic species dwelling in this habitat. Although there is some evidence of the species use of caves in history, the bibliography of these last two centuries indicates a progressively

increasing use of coastal caves with entrances having limited human access. It has therefore been speculated that the species use of this habitat, to rest, moult its fur, give birth and nurse its pup has been an adaptation to the intense human persecution to which it has been exposed since classical antiquity. The species uses coastal caves with underwater or semi-submerged entrances, provided that these are characterized by emerged internal beaches or rocky platforms on which the species may haul-out (Reijnders *et al.*, 1997).

Caves used by monk seals for breeding purposes have specific characteristics, they need to be well protected from wind and waves and human disturbance in order to guarantee pup survival. This implies the presence of factors such as: an entrance with a protective barrier against strong waves, a long entrance corridor, a well sheltered shallow internal pool, beaches that are always above high tide level, a chamber with a wide beach or with a highly inclined beach (Gücü *et al.*, 2004; Karamanlidis *et al.*, 2004; Dendrinos *et al.*, 2007).
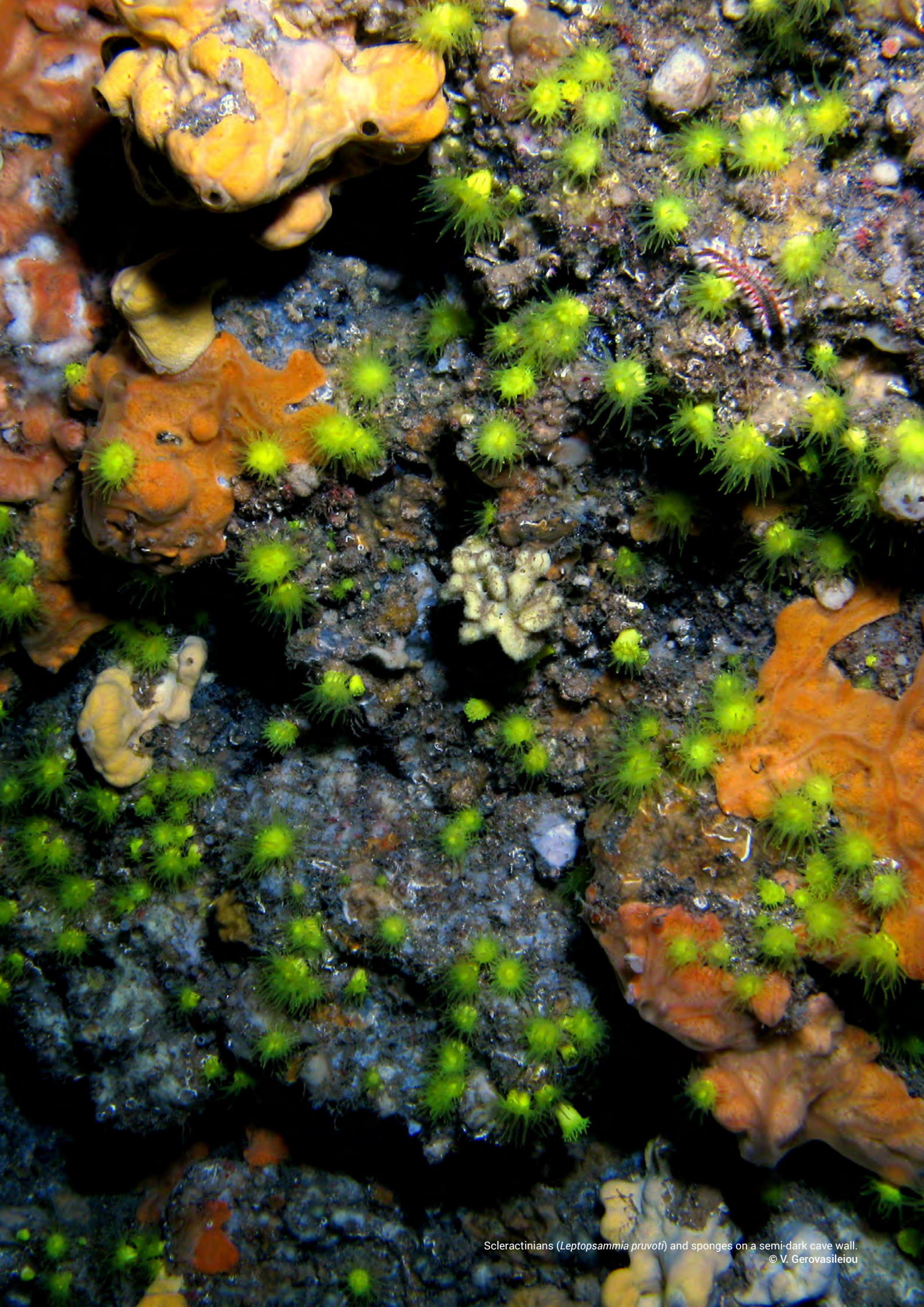
Scleractinians (*Leptopsammia pruvoti*) and sponges on a semi-dark cave wall.
© V. Gerovasileiou

The shrimp *Palaemon serratus* is one of the most common decapod species in marine caves.
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9. CONSERVATION VALUE & CURRENT THREATS

9.1. Conservation value

Marine caves are acknowledged as "refuge habitats" or "biodiversity reservoirs" of great conservation value, harbouring a rich biodiversity (40-65% of the Mediterranean sponge, bryozoan, tardigrade and brachiopod diversity), including a considerable number of rare, cave-exclusive, endangered, protected, and deep-sea species (Harmelin *et al.*, 1985; Gerovasileiou & Voultsiadou, 2012, 2014; Gerovasileiou *et al.*, 2015a; Rosso & Di Martino, 2016). Among the most emblematic species dwelling in this habitat type, are the Mediterranean monk seal *Monachus monachus* and the red coral *Corallium rubrum*, both listed as endangered (EN) in the IUCN Red List of Threatened Species. The survival of important seal populations in the North-Eastern Mediterranean, especially in the Aegean Sea, is related to the availability of high numbers of suitable cave habitats across the coasts and insular areas of the region (Voultsiadou *et al.*, 2013) coupled to the extensive coastline of the insular locations which provide protection from human disturbance and prevailing winds. Considering that the species has a very prolonged lactation period (Pastor & Aguilar, 2003), marine caves represent a habitat of high conservation value for the survival of the species. The red coral has been traditionally considered a typical species of the semi-dark cave biocoenosis, where it can form dense facies (Pérès & Picard, 1964). Recent studies have suggested that the cave habitat provides natural protection from possible human induced disturbances, as shown by the finding of abundant and healthy populations, compared with exposed habitats, in caves of Marseille and Corsica (Garrabou *et al.*, 2001; Garrabou *et al.*, 2017). Several other protected species listed in Annex II of the Bern Convention and the SPA/BD Protocol of the Barcelona Convention, are commonly found in caves, such as the orange coral *Astroides calycularis*, the gastropods *Erosaria spurca* and *Luria lurida*, the date mussel *Lithophaga lithophaga*, the hatpin urchin *Centrostephanus longispinus*, the slipper lobster *Scyllarides latus* and the brown meagre *Sciaena umbra*. In addition, all protected sponges are also found in caves, including the deep-water species *Lycopodina hypogea*, which was first described from the famous 3PP Cave of Marseille (Vacelet & Boury-Esnault, 1996), and typical cave-dwelling species, such as the relict calcareous sponge *Petrobiona massiliana* and the demosponge *Aplysina cavernicola*. The four Mediterranean bath sponges, listed in Annex III of the Bern and Barcelona Conventions, which were recently classified as endangered at the regional level of the Aegean Sea (Gerovasileiou *et al.*, 2018), have been reported from numerous marine caves (e.g. *Spongia officinalis* is reported from >30 Mediterranean caves; Gerovasileiou & Voultsiadou, 2012; Manconi *et al.*, 2013).

Several benthic taxa are considered, so far, exclusive to this key habitat; most of these are recorded from a small number or only from a single marine cave (Gerovasileiou & Voultsiadou, 2012), although future research could show that some could be also distributed in other cryptic or deep-sea habitats. Thus, marine caves have been characterized as "natural laboratories" or "deep-sea mesocosms" in the littoral zone, because they provide direct human access to bathyal-like conditions in the scuba diving zone (Harmelin & Vacelet, 1997; see sub-section 6.1.4). In addition to the cave-exclusive and deep-sea faunal elements, marine caves harbour a considerable percentage of the total Mediterranean endemic fauna (e.g. 41% of the Mediterranean endemic sponges; Gerovasileiou & Voultsiadou, 2012). This does not only concern sessile taxa, but motile fauna as well, such as the rare gobids *Corcyrogobius liechtensteini*, *Didogobius splechtnai*, *Gammogobius steinitzi* and *Speleogobius trigloides*, which dwell in marine caves and other cryptic habitats (Bussotti *et al.*, 2015 and references therein).

The presence of caves in rocky coasts has been suggested to provide additional resources for fishes (e.g. food availability, refuge against predators, sand patches within a rocky matrix) compared to rocky reefs without caves, thus affecting local species richness and distribution patterns (Bussotti & Guidetti, 2009; Bussotti *et al.*, 2015). Several fishes and crustaceans which seek for shelter in marine caves (e.g. during cold seasons) or use them occasionally as nursery habitats, are of commercial interest (Gerovasileiou *et al.*, 2015a). Furthermore, recent studies showed that cave biota (e.g. sessile taxa and microbial mats) present potential interest in the fields of biotechnology, as sources of bioactive substances (Uriz *et al.*, 1991; Martí *et al.*, 2005; Turon *et al.*, 2009; Audoin *et al.*, 2013), but also bioenergy and bioremediation (Polymenakou *et al.*, 2018).

The rich and unique biodiversity of marine caves, coupled with their geomorphological complexity and high aesthetic value, make them popular "hot-spots" for marine-based recreational activities (Rovere *et al.*, 2011; Salomidi *et al.*, 2012), such as boat tours, snorkelling and SCUBA diving throughout the Mediterranean basin. In addition, a number of marine caves were found to present paleontological, archaeological and paleo-climatological interest (e.g. Antonioli *et al.*, 2001; Poulakakis *et al.*, 2002; Collina-Girard, 2004).

For all the above reasons, marine caves are protected by the EU Habitats Directive (92/43/EEC – habitat code 8330 "Submerged or partially submerged sea caves") and, at the Mediterranean level, under the "Action Plan for the conservation of the coralligenous and other

calcareous bio-concretions"[16] (UNEP-MAP-RAC/SPA, 2008) and the "Dark Habitats Action Plan" for the conservation of habitats and species associated with seamounts, underwater caves and canyons, aphotic hard beds and chemo-synthetic phenomena in the Mediterranean Sea of the Barcelona Convention (UNEP-MAP-RAC/SPA, 2015). The number of marine caves included in Marine Protected Areas (MPAs) is unknown, although the habitat is represented in 33 Mediterranean MPAs (Abdulla *et al.*, 2008).

9.2. Threats and impacts

Marine caves are fragile ecosystems, vulnerable to both natural and human disturbances (Giakoumi *et al.*, 2013; Rastorgueff *et al.*, 2015a). Severe storm waves can occasionally reach the inner parts of the caves, bringing in sediment and detritus and abrading walls and ceilings, thus causing mortality of the cave-dwelling organisms. Marine heat waves, which cannot be considered as a natural disturbance, as the present sea water warming is mostly of anthropogenic origin (Bianchi, 2007), have been shown to cause important modifications on both the motile and the sessile components of the cave community (Chevaldonné & Lejeusne, 2003; Parravicini *et al.*, 2010; Costa *et al.*, 2018; Sempere-Valverde *et al.*, 2019).

Despite being difficult to access, when compared to open sea habitats, there is increasing evidence of local impacts caused by human activities, such as illegal red coral harvesting, spearfishing (e.g. *Sciaena umbra* and *Phycis phycis*), urbanization and construction of coastal structures, waste outflows, litter and multiple unregulated visits by tourist boats and divers (Di Franco *et al.*, 2010; Guarnieri *et al.*, 2012; Giakoumi *et al.*, 2013; Rastorgueff *et al.*, 2015a; Nepote *et al.*, 2017; Mačić *et al.*, 2018; Sempere-Valverde *et al.*, 2019). Sessile benthic communities in marine caves have low recovery potential, since the development of communities in a "mature" state could take more than a decade (Harmelin, 1980; Harmelin *et al.*, 1985; Rastorgueff *et al.*, 2015a; see chapter 7). Several sessile invertebrates with erect morphologies, as well as their bioconstructions, are slow-growing, fragile, and thus highly vulnerable to mechanical damages caused by unintentional contact with divers, which are more likely to happen in caves and overhangs. Sediment re-suspension and accumulation of exhaled air bubbles at the cave ceiling can be also have detrimental effects on sessile filter feeders (Milazzo *et al.*, 2002; Lloret *et al.*, 2006; Di Franco *et al.*, 2010; Guarnieri *et al.*, 2012; Burgués *et al.*, 2016). Coastal constructions (e.g. jetties) alter sediment transport, and may cause sediment deposit in the innermost part of the caves, with consequent suffocation of the encrusting fauna (Nepote *et al.*, 2017; Montefalcone *et al.*, 2018).

An additional potential threat to Mediterranean marine cave communities is related to the continuous spreading of non-indigenous species, especially in the eastern and southern regions. A total of 56 non-indigenous (NIS) and cryptogenic taxa have been reported so far from approximately 50 marine caves and tunnels of the Mediterranean (Gerovasileiou *et al.*, 2016c), including molluscs (15), cnidarians (9), bryozoans (7), polychaetes, crustaceans (6), macroalgae, fishes (3) and tunicates (2). Most of these taxa (66%) were found in caves of the South-eastern Levantine Sea (mainly in Lebanon, e.g. Bitar in Zenetos *et al.*, 2015), with shipping and Lessepsian migration through Suez Canal being their main pathways of introduction. These taxa were mostly reported from the entrance and semi-dark zones of shallow and semi-submerged caves and tunnels. The impacts of these taxa on native cave dwellers have not been investigated to date. Nevertheless, their presence in most studied marine caves of the Levantine Sea, and the population explosion of alien fishes (e.g. *Pempheris rhomboidea*) in caves of this area should be further studied and monitored (Gerovasileiou *et al.*, 2016c).

9.3. Conservation priorities and suggestions

Marine cave communities are characterized by high levels of "individuality", generated by cave-specific topographical features (Bussotti *et al.*, 2006), but also by large-scale biogeographic heterogeneity, with several cave-exclusive and rare taxa recorded only from a few or a single marine cave (Gerovasileiou & Voultsiadou, 2012; see sub-section 5.1). This points to the need for protecting marine caves of different morphological types in different biogeographic regions, in order to address small and large-scale heterogeneity, thus safeguarding maximum representation of diversity aspects (Gerovasileiou & Voultsiadou, 2012; Giakoumi *et al.*, 2013). Special priority should be given to: particular cave types or caves with geomorphological features and micro-habitats that could harbour unique communities (e.g. anchialine caves, marine caves with sulphur or internal freshwater springs, those having a descending profile or vertical pits); caves harbouring cave-exclusive, relict and rare species (e.g. steno-endemics); caves harbouring protected, threatened and commercial species; caves with high species richness and functional diversity. In addition, given that cave ecosystems largely depend on external trophic inputs and larval supply from nearby environments (Harmelin *et al.*, 1985; Fichez, 1990b; Benedetti-Cecchi *et al.*, 1997; see chapter 6), it is important to safeguard good ecological status and maintain connectivity with nearby habitats (e.g. rocky reefs and *Posidonia* meadows) in conservation planning.

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[16] Coralligenous and semi-dark cave communities have been integrated into the Action Plan for the conservation of the coralligenous and other calcareous bio-concretions in the Mediterranean Sea (UNEP-MAP-RAC/SPA, 2008).

Sponge-dominated assemblage in a semi-dark cave biocoenosis.
© V. Gerovasileiou

Semi-dark cave assemblage.
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10. GAPS OF SCIENTIFIC KNOWLEDGE & FUTURE RESEARCH DIRECTIONS

Despite the fact that marine caves of the Mediterranean Sea have been studied for their fauna more intensively than those in any other area of the world ocean (Gerovasileiou & Voultsiadou, 2016), there are still important gaps in our knowledge regarding their distribution, biodiversity, ecosystem structure and functioning, dynamics, ecological status, impact and management potential.

Previous overviews on Mediterranean marine caves (Bianchi *et al.*, 1996; Cicogna *et al.*, 2003; Gerovasileiou & Voultsiadou, 2012, 2014; Gerovasileiou *et al.*, 2015a) highlighted that information on their distribution and biodiversity remained highly scattered and fragmented. In addition, during the data compilation process of the above reviews, several gaps and limitations came up, such as: (i) lack of spatial (coordinates) and geomorphological (e.g. depth and cave type) information about numerous marine caves; (ii) several caves having the same toponyms (e.g. Blue Cave/Grotta Azzurra) and reports on single sites with multiple caves (unspecified number); (iii) lack of ecological information (e.g. cave zone and depth) about several taxa recorded from caves; (iv) lacking or limited data about particular geographic areas, cave types and taxa; and (v) taxonomic inconsistencies (e.g. synonymies and possible misidentifications). The recent development of online open access biodiversity information systems, such as the World Register for marine Cave Species (WoRCS) thematic database (Gerovasileiou *et al.*, 2016b) and synergies between parallel initiatives, regional (sub-)registers and infrastructures, provide the platforms and tools in order to catalogue, quality control and eventually mobilize datasets (e.g. georeferenced, taxonomically updated species lists accompanied by relevant meta-data). In addition, citizen science initiatives could significantly contribute to increase data availability on the distribution and biodiversity of marine caves, and possibly their monitoring, especially in understudied areas.

Based on the gaps identified during previous and present overviews, it is recommended that future marine cave research should focus on:

• Filling regional knowledge gaps, e.g. baseline studies and inventories in understudied Southern and Eastern Mediterranean areas, such as the North African, Aegean and Levantine coasts.

• Filling thematic gaps regarding particular groups of biota (e.g. microbial diversity, meiofaunal taxa), cave assemblages and formations (e.g. sediment infauna and bioconstructions), deeper caves (in the circalittoral zone and in deep waters) and peculiar cave types (e.g. anchialine caves and caves with hydrothermal activity, cold seeps and freshwater springs).

• Understanding and monitoring ecosystem structure and functioning (e.g. biotic interactions) and revisiting previously studied caves in order to assess potential changes and impacts caused by different drivers (e.g. water temperature rise, non-indigenous species, recreational visits).

• Investing on multi-disciplinary, integrated approaches and capacity building in order to better understand abiotic-biotic interactions, impacts or even to investigate potential applications in the framework of the Blue Growth sectors (e.g. biotechnology).

• Investigating and applying management and restoration options/protocols, at different spatial scales in order to achieve future conservation targets.
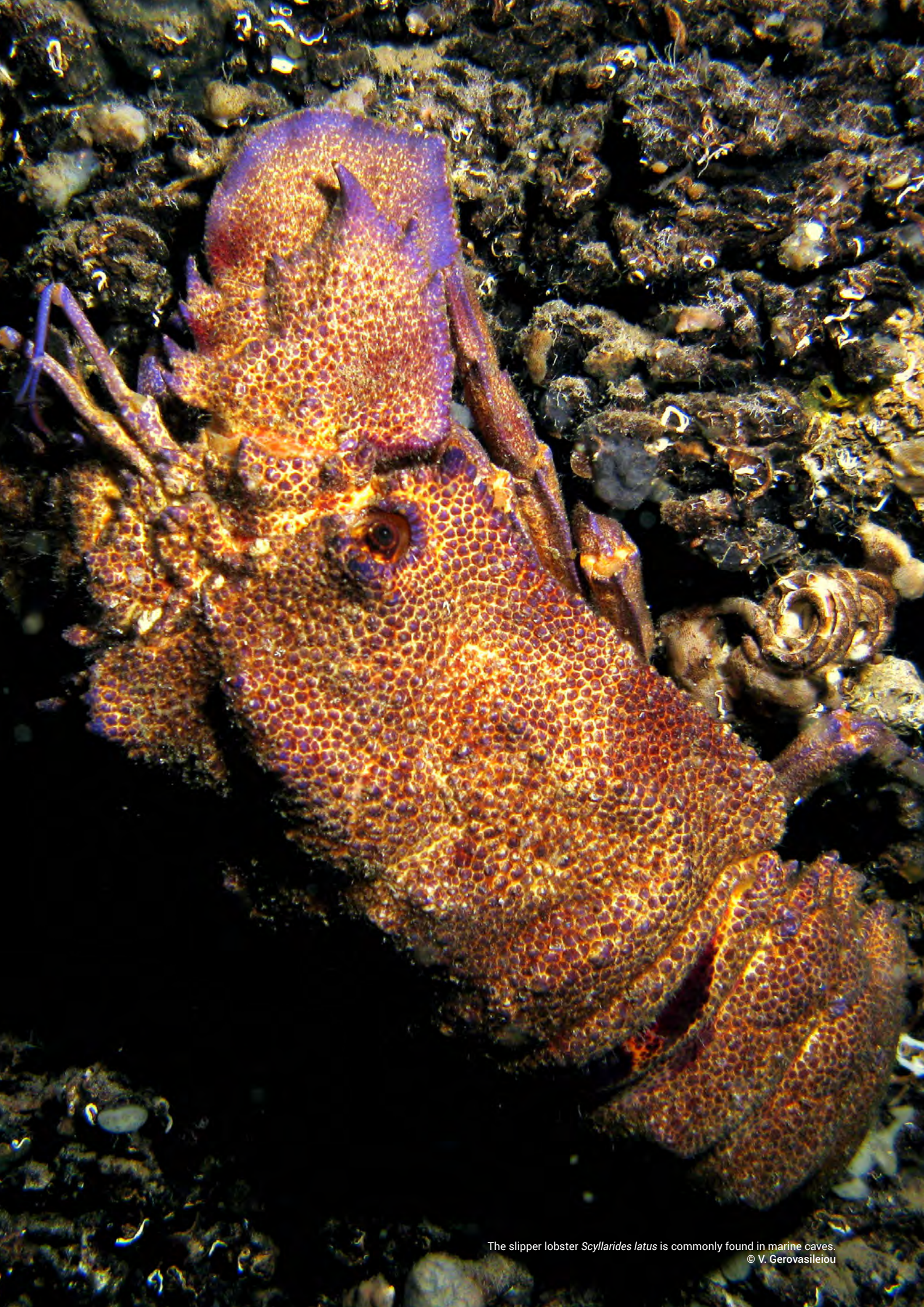
The slipper lobster *Scyllarides latus* is commonly found in marine caves.
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