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MEDITERRANEAN MARINE CAVES: A SYNTHESIS OF CURRENT KNOWLEDGE

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Abstract Marine caves are biodiversity reservoirs and refuge habitats, harbouring rare species and living fossils. The Mediterranean Sea hosts more than 3000 caves, which are among the most studied in the world. This review aims to synthesize and update knowledge of Mediterranean marine caves. Their biota includes few obligate cave-dwelling organisms, but many cryptobiotic or crevicular (crevice-dwelling) and bathyphilic (preferring deep-water) species that secondarily colonize caves. A total of 2369 taxa have been reported from 404 caves in 15 countries, with several species new to science described in recent decades. Dramatic environmental gradients generate a zonation of the biota, with up to six faunal zones and two main biocoenoses. Biotic cover and biomass are strongly reduced inside caves, due to hydrological confinement and trophic depletion. The food web is based on suspension-feeders, but motile carnivores play a role in the importation of organic matter from outside. Lack of primary production, faunal affinities and microbial metabolism make marine caves readily accessible models of deep ocean ecosystems. Future research should focus on filling regional (e.g. south-eastern Mediterranean) and thematic (e.g. microbes, meiofauna, macro-infauna) gaps in fundamental knowledge, and on management measures. Marine caves have low ecological resilience and harbour many species of conservation interest, but are threatened by seawater warming, local human impacts and non-indigenous species.

Keywords: Marine Caves; Benthic Habitats; Biodiversity; Conservation; Mediterranean Sea

Introduction

Rocky reefs, coastal cliffs and coral reefs around the world harbour cavities of various sizes at or below sea level, and therefore contain marine water (Colantoni 1978). These ‘marine caves’ are a quantitatively trivial fraction of the marine environment but hold a great scientific and ecological importance, as they represent a major reservoir of marine biodiversity (Gerovasileiou & Voultsiadou 2012, Gerovasileiou et al. 2016a) and provide ecosystem services to humans (Salomidi et al. 2012).

Land caves have played a major role in the life and evolution of humans: over the centuries, they have offered shelter to humans and their domestic animals, and have been important for religion and culture; today, they provide opportunities for sport adventures, with research and scientific knowledge fostered by these activities. On the contrary, marine caves began to be explored much later and explicitly for scientific reasons. After early attempts in the eighteenth century, when the Italian

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naturalist Filippo Cavolini reached submerged caves near Sorrento (Bay of Naples, Italy) with the aid of rudimentary equipment (Bianchi & Morri 2000), the scientific community addressed the study of marine caves especially in the middle of the twentieth century, motivated by the expectation of extraordinary new findings: "we will show you … things you did not even dream about" (Riedl 1978). The ensuing discovery of the many peculiarities and the natural heritage value of marine caves gave birth to the awareness of the need for their conservation, as they turned out to be unique and vulnerable habitats threatened by multiple global and local pressures (Montefalcone et al. 2018). The first instances of protection date back to the 1970s (Sarà 1974, 1978) but only recently have led to concrete initiatives (at least in Europe and the Mediterranean) by the Habitats Directive of the European Union and by the Mediterranean Action Plan of the United Nations Environment Programme. About two-thirds of the Mediterranean marine protected areas include marine caves (Abdulla et al. 2008).

The rocky coasts of the Mediterranean Sea are particularly rich in marine caves (Hofrichter 2002, Giakoumi et al. 2013), whose geology, biology and ecology have been studied with continuity for several decades (Riedl 1966, Cattaneo & Pastorino 1974, Harmelin et al. 1985, Bianchi et al. 1996, Cicogna et al. 2003, Gerovasileiou et al. 2015a). Environmental issues about Mediterranean marine caves have been recently tackled to evaluate their health status (Rastorgueff et al. 2015a) and to evidence threats (Gerovasileiou et al. 2016b, Nepote et al. 2017, Montefalcone et al. 2018). Thus, Mediterranean marine caves are perhaps the best known of the world ocean (Gerovasileiou & Voultsiadou 2016) and may offer paradigms and theory to students of marine caves from other geographic regions.

This review aims to synthesize and update existing knowledge about Mediterranean marine caves, to evaluate the current scientific knowledge and to illustrate the need for the protection of, and research on, these habitats: only a small number of caves have been explored and, mostly, in a superficial and incomplete manner, while it is likely that many caves are as yet undiscovered. We largely based our review on previous reviews, often written in language other than English (e.g. German: Riedl 1966, French: Harmelin et al. 1985; Italian: Bianchi et al. 1996; Greek: Gerovasileiou 2014) and therefore less accessible to the international audience. Recent additions have been possible thanks to a large number of publications dispersed in various scientific journals and in the grey literature, and to a recent Turkish volume (Öztürk 2019). The bulk of our text derives, with modification, from a desktop study prepared for the Regional Activity Centre for Specially Protected Areas of the United Nation Environment Programme Mediterranean Action Plan (Gerovasileiou & Bianchi 2020).

Marine caves and cave biota

The term 'cave' is commonly used to describe an opening into a natural underground or underwater hollow, which is large enough for a human to enter (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. 2016a). They are formed by different processes in various rock types, such as dissolution of bedrock by water circulating through fissures and pores ('solution' or 'karsts' caves), fracturing, differential non-dissolution erosion, lava tubes and talus caves among rock falls. In marine caves (also known as 'littoral' or 'sea caves'), the mechanical action by the waves may also be important (Riedl 1966, Colantoni 1978, 1994, 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 below sea level – see Surić et al. 2010). Bianchi et al. (1996) defined 'marine cave' as a cavity of various origins, entirely or partly occupied by the sea, accessible to humans, 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.

A standard glossary, based on existing terminology for marine cave systems and their biota, has recently been developed by the Editorial Team of the World Register of marine Cave Species (WoRCS) database (see Gerovasileiou et al. 2016a, 2020). Marine caves belong to several types (Figure 1). They can be assigned to two main categories according to their submersion level: 'submerged', completely below the water level; and 'semi-submerged', extending above and below the sea surface, and thus more exposed to and affected by sea-surface dynamics. Cave morphology can also be 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 caves with negligible horizontal passages) or more complex morphologies, consisting of arrays of intersecting passageways that form distinctive patterns (Riedl 1966, Palmer 1991, Field 1999, Hofrichter 2002, Gerovasileiou et al. 2016a). The term 'anchialine' or 'anchihaline' derives from the Greek word '*άγχίαλος*' (= near the sea) and is used to characterize environments that are supplied with saline or brackish groundwater of marine origin, through an underground connection to the sea (Stock et al. 1986, Gerovasileiou et al. 2016a). 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, Bianchi et al. 1996).

Cave biota can be assigned to four main ecological categories (Delamare Deboutteville 1971, Culver & Pipan 2009, Romero 2009, Culver & White 2012, Gerovasileiou et al. 2016a,

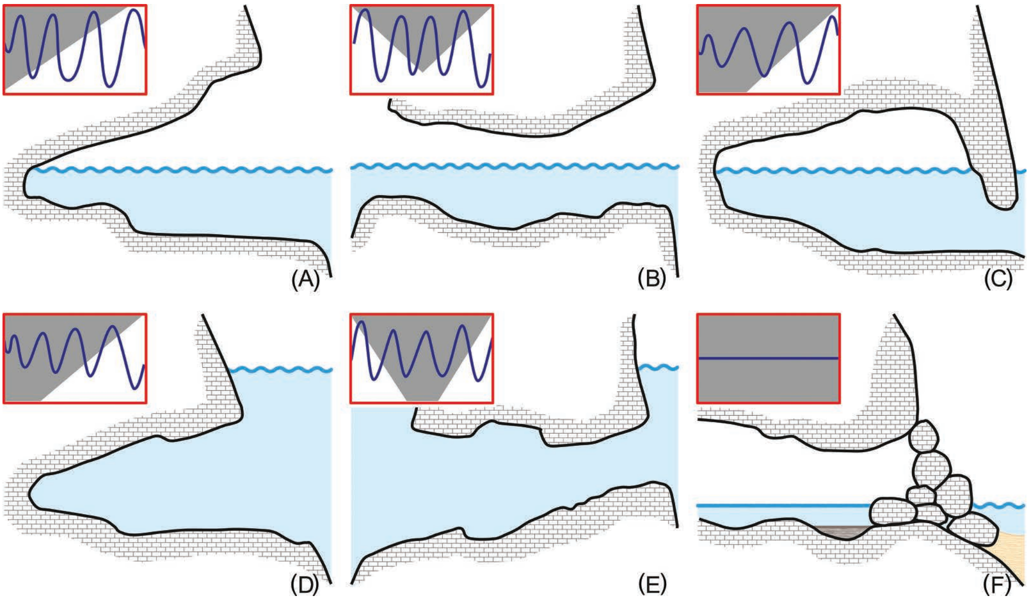

Figure 1 Basic morphological types of marine caves (in the broad sense): (A) semi-submerged blind-ended (cul-de-sac) cave; (B) semi-submerged tunnel; (C) cave with air dome; (D) submerged blind-ended cave; (E) submerged tunnel; and (F) marginal cave. Complex caves may show a combination of two or more basic types. Upper left boxes schematize the patterns of light penetration (white portions with respect to grey portions) and water movement (sinusoidal curves) inside the different types of cave. Redrawn and modified from Riedl (1966) and Hofrichter (2002).

Lunghi & Manenti 2020): ‘troglobionts’ or ‘stygobionts’ (cave-exclusives *sensu lato*), which are obligatory cavernicoles, adapted to subterranean life (e.g. by loss of pigmentation and vision); ‘troglophiles’ or ‘stygophiles’, which 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); ‘trogloxenes’ or ‘stygoxenes’, 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 leaving to forage in nearby habitats during night); ‘accidental’ (or random visitors), which may enter caves by chance (e.g. advected by currents), but can only survive in this environment for short periods of time. The prefix ‘troglo-’ should be preferred for subterranean species and ‘stygo-’ for the aquatic cave biota.

In contrast to terrestrial and anchialine caves, marine caves *sensu stricto* 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 marine caves could be characterized as stygophiles (e.g. sponges and bryozoans which also occur in dim-light environments outside caves, such as coralligenous reefs and deep waters) or stygoxenes (e.g. crustaceans and fishes exhibiting diel, also known as nychthemeral, movements into and out of 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’ or ‘crevicular’ (i.e. preferring cryptic habitats such as rock crevices) and ‘bathyphilic’ species in marine caves is at the root of the concept of ‘secondary troglobiosis’ (Cattaneo & Pastorino 1974) or, better, ‘secondary stygobiosis’, since these species originate from external marine environments (such as coralligenous reefs, deep rocks and small hard substrata dispersed in detrital infralittoral and circalittoral bottoms) but are commonly found in marine caves (Figure 2), and therefore become characteristic of this habitat only secondarily (Iliffe 1990). Nonetheless, a considerable number of taxa have not been – at least yet – reported from habitats other than caves and thus can be considered as exclusive to caves in the broad sense: future research, for instance in cryptic and deep-sea habitats, might show that some of these species occur in other habitats (Gerovasileiou & Voultsiadou 2012). Since the 1980s, the scientific exploration of underwater caves, and especially those of the

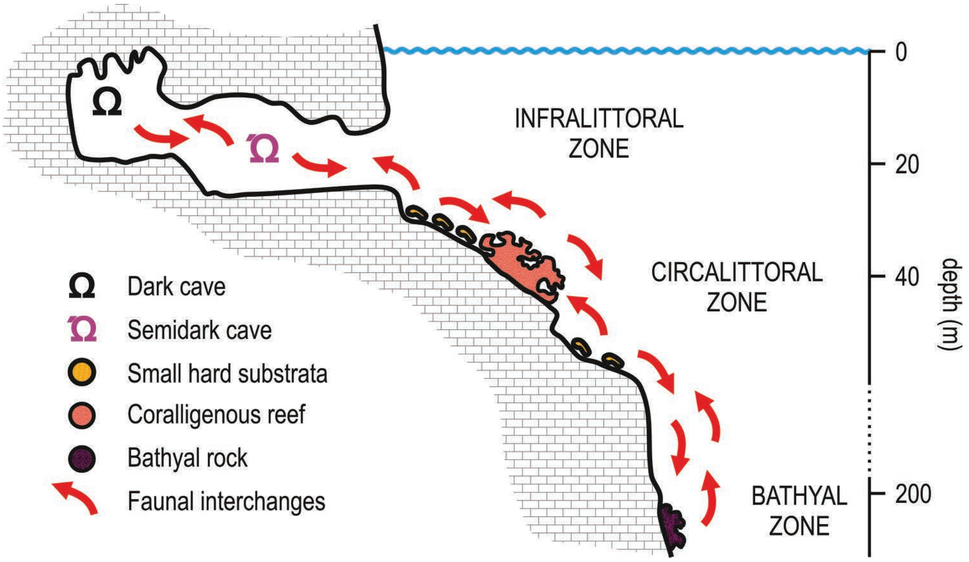

Figure 2 A schematic representation of the faunal interchanges between marine caves and the external environments, allowing cryptobiotic/crevicular and bathyphilic species to colonize the caves (secondary stygobiosis) and providing opportunity for cave species to disperse. Redrawn and modified from Harmelin (1986) and Bianchi et al. (1996).

anchialine type, has led to outstanding discoveries of novel taxa that exhibit unique adaptations to cave life (Iliffe et al. 1983, Stock 1994, Iliffe & Kornicker 2009, Gerovasileiou et al. 2016a and references therein). It is possible that some of these taxa are the result of ecological specialization from generalists that penetrated caves from external environments in the past, including 'relict species' or palaeoendemics, e.g. remnants of the (sub)tropical fauna that thrived in the Mediterranean Sea during warm periods of its history (Bianchi et al. 2012b) and found refuge and survived in cave habitats (Harmelin et al. 1985, Pérez et al. 2004). Major examples include the brachiopod *Tethyrynchia mediterranea* (Logan et al. 2004) and the serpulid *Marifugia cavatica* (Bianchi & Sanfilippo 2003).

Distribution

Rock constitutes more than half (54%) of the Mediterranean coastline (Stewart & Morhange 2009), limestone being one of the most common types (Lewin & Woodward 2009). Through time, the ongoing geological processes (e.g. karstic phenomena) in this semi-enclosed sea have resulted in the formation of a large number of more or less complex marine and anchialine cave systems (Gerovasileiou & Voultsiadou 2012). According to the latest inventory by Giakoumi et al. (2013) and the present study (Figure 3), there are more than 3000 marine caves in the Mediterranean, the majority of which are located in the eastern Adriatic, Aegean, Tyrrhenian, Provençal and Ionian coasts (Table 1), where they are sometimes densely concentrated in islands and rocky peninsulas (e.g. Aegean Archipelago, Croatian and Balearic islands, Corsica and Sardinia, Sorrentine Peninsula, Cape Palinuro, Salento).

At local or regional scales, there has been detailed mapping of marine caves in Italy (Cicogna et al. 2003), Corsica (Anonymous 2010), Croatia (Surić et al. 2010) and Greece (Sini et al. 2017). In addition, recent expeditions and baseline studies in the framework of the research projects MedKeyHabitats, MedMPAnet and LIFE BaĦAR for N2K have provided valuable information on the distribution of marine caves, their biodiversity and impending threats in previously understudied regions of the Mediterranean Sea. For example, a number of caves, tunnels and numerous

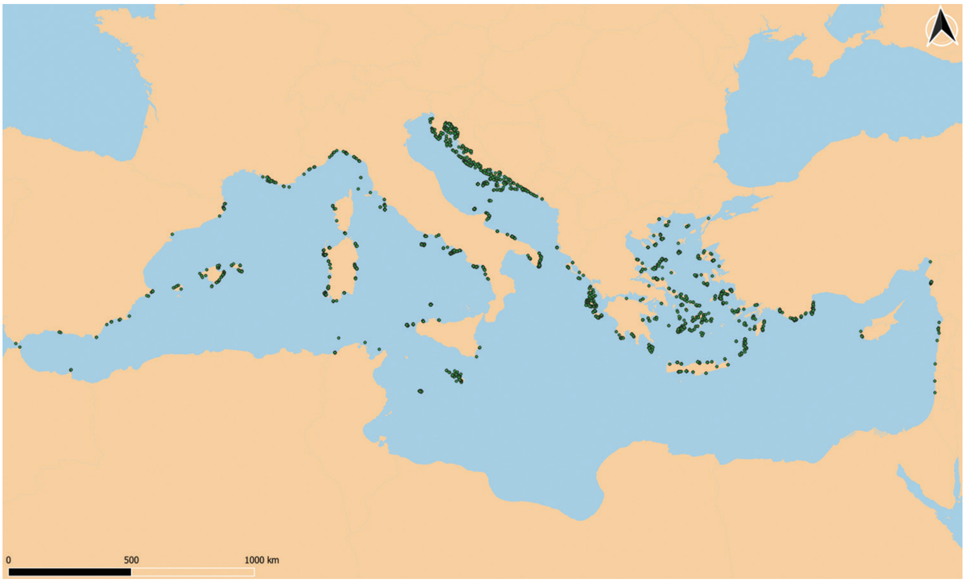

Figure 3 Distribution of known marine caves (green dots) in the Mediterranean Sea (based on data from Giakoumi et al. 2013, Sini et al. 2017 and LIFE BaĦAR for N2K project – LIFE12 NAT/MT/000845). Note the scarcity of data from the southern coasts.

Table 1 Number of marine caves recorded by Mediterranean ecoregion

Mediterranean ecoregion	Number of marine caves
Alboran Sea	24
Algero-Provençal Basin	459
Tyrrhenian Sea	581
Tunisian Plateau/Gulf of Sidra	141
Adriatic Sea	708
Ionian Sea	307
Aegean Sea	622
Levantine Sea	209

Sources: Giakoumi et al. (2013), Sini et al. (2017), LIFE BaĦAR for N2K project (LIFE12 NAT/MT/000845) and new data from this study.

small caverns were recorded in Cap des Trois Fourches and Jbel Moussa, in Morocco (Bazairi et al. 2012, 2013, 2016, Anonymous 2014) and in the island of Rachgoun, in Algeria (Ramos Esplá et al. 2016). In Lebanon, Raoucheh Cave and other caves in Ras Chekaa and Naqoura regions were studied within MedMPAnet project (Ramos-Esplá et al. 2012, 2013, 2014). Within MedMPAnet and MedKeyHabitats projects, marine caves were also recorded and studied in the Adriatic Sea: small midlittoral caves in Albania (Kashta et al. 2013) and large marine caves in the Platamuni region of Montenegro (Torchia et al. 2016a,b, Mačić et al. 2019). In Malta and Gozo Islands, the project LIFE BaĦAR for N2K shed light on numerous marine caves and tunnels (37 semi- and 52 fully submerged caves) of various sizes and depth, as well as 17 deep-water caves between 205 m and 795 m (Borg et al. 2017). A considerable number of marine caves from the Aegean and Levantine coasts of Turkey were described in a publication by the Turkish Marine Research Foundation (Öztürk 2019). The above projects and baseline studies have greatly contributed to filling regional gaps of knowledge from previously understudied marine regions and led to the proposal or even the establishment of new marine protected areas.

Given the logistic constraints involved in finding and surveying marine caves, especially the fully submerged ones, their number is assumed to be much higher at both Mediterranean and local scales, and mapping efforts are required in order to fill current distribution gaps in the eastern and southern Mediterranean regions. Detailed guidelines for compiling inventories of dark habitats, including marine caves, have recently been provided by Gerovasileiou et al. (2017a).

Most existing marine cave records correspond to shallow and/or semi-submerged caves, with a water depth that rarely exceeds 15 m, as they are generally easier to detect and access by both scientists and recreational divers. Information about deeper caves is limited, with only a small number of marine caves studied for their biota in the depth range 15–40 m (Gerovasileiou & Voultsiadou 2012, Canessa et al. 2014). However, bathymetric data are lacking in several cases. The recent study of deeper areas with the use of Remotely Operated Vehicles (ROVs) has shown that hard substrata in deeper waters can also have large overhangs and cavities. For instance, deep-water caves and large overhangs have recently been 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, ~5.96–5.33 Ma (Evans et al. 2016, Borg et al. 2017). However, their study is logistically difficult and constitutes a challenge for future explorations.

The biological study of Mediterranean marine caves

In contrast to terrestrial caves, their marine counterparts remained virtually unexplored until the second half of the twentieth century. Their study became possible only after the development of autonomous diving, which allowed not only cave exploration but also direct observation and sampling by marine scientists (Laborel 1960, Vacelet 1967, Riedl 1978, Cattaneo-Vietti & Mojetta 2021). Technological advances in autonomous diving, from the development of the first reliable open-circuit self-contained underwater breathing apparatus in 1942–1943 (Drach 1948) to the modern closed-circuit rebreathers (Iliffe & Bowen 2001), have facilitated underwater cave research and revealed unique fauna (e.g. Jaume & Boxshall 2005, Iliffe & Kornicker 2009).

In the Mediterranean basin, the first thorough studies of marine caves and their biota were conducted by French (Pérès & Picard 1949, 1955, Corroy et al. 1958, Laborel & Vacelet 1958, 1959), Austrian (Starmühlner 1955a,b, Abel 1959, Banse 1959, Riedl 1959a,b,c,d,e,f, 1966, Russ & Rützler 1959, Rützler 1965, etc.) and Italian scientists (e.g. Sarà 1958, 1959a, 1961a,b, 1962, 1968, 1974, 1978, Cattaneo & Pastorino 1974, Cinelli et al. 1977, Cantone et al. 1979), followed by contributions from Spanish scientists in the 1980s (Bibiloni & Gili 1982, Gili et al. 1982, 1986, Bibiloni et al. 1984), and by Croatian scientists since 2000 (e.g. Arko-Pijevac et al. 2001, Bakran-Petricioli et al. 2007, 2012, Radolović et al. 2015, Petricioli & Bakran-Petricioli 2019). Studies of marine caves in the eastern Mediterranean were published more recently by Greek (Gerovasileiou 2014, Gerovasileiou et al. 2015a and references therein, Gerovasileiou & Voultsiadou 2016, Gerovasileiou et al. 2017b, Dimarchopoulou et al. 2018) and Turkish scientists (Öztürk 2019), with contributions also from Cyprus (Guido et al. 2017a, Jimenez et al. 2019) and Lebanon (Pérez et al. 2004, Ramos-Esplá et al. 2012, Castelló et al. 2020).

A major 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 the first synthesis of existing knowledge acquired in the 1950s and 1960s. Much of the information came from the 'Tyrrhenia-Expedition', which started in 1952 and focused on marine caves in the region of Naples, Italy. Subsequently, important reviews about the biology of marine caves were published in France (Harmelin et al. 1985), Italy (Bianchi 1994, 2003, Bianchi et al. 1996, Cicogna et al. 2003) and the eastern Mediterranean Sea (Gerovasileiou et al. 2015a), while Gerovasileiou & Voultsiadou (2012) and Bussotti et al. (2015) provided overviews of the sponge and fish fauna of marine caves, respectively, at the Mediterranean scale.

Taxonomic studies

The first approach to the biological study of marine caves – as of other habitats – was undoubtedly a taxonomic one, an 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, 1997a, 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, Melis et al. 2016, 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 (Pretus 1990, Fransen 1991), Mysida (Alcaraz et al. 1986, Wittmann 2004), Thermosbaenacea (Wagner & Chevaldonné 2020), Polychaeta (Zibrowius 1968, Fassari & Mòllica 1991), Gastropoda (Warén et al. 1997, Palazzi & Villari 2001, Crocetta et al. 2020), Bivalvia (La Perna 1998, 1999), Tardigrada (Villora-Moreno 1996), Bryozoa (Hayward 1974, Silén & Harmelin 1976, Harmelin et al. 2007, Rosso et al. 2020a), Brachiopoda (Logan & Zibrowius 1994), Chaetognatha (Casanova 1986) and Pisces (Kovačić 1999).

Moreover, the study of marine cave biota revealed that these 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, Rosso et al. 2013a, Pisera & Gerovasileiou 2021), triggering further taxonomic and ecological studies. In addition to the biodiversity inventories, the notable small-scale environmental gradients in marine caves, as well as their influence on the spatial variability of biota, became a subject of research from the first pioneer bionomic studies until today.

Bionomic descriptions

In most English dictionaries, bionomy (or bionomics), from the Greek '*βίος*', life, and '*νόμος*', law, is synonymous with ecology. In the tradition of Mediterranean ecology, however, bionomy refers specifically to the part of ecology that studies the distribution of organisms and their assemblages along ecological gradients to identify zones and to understand the link between habitats and species (Bianchi et al. 2012a).

The typology and distribution of benthic communities in Mediterranean marine caves has been mostly studied by French, Austrian and Italian scientists. The first description of the marine cave communities was published by Pérès & Picard (1949), who studied Niolon Cave (Marseille region, France) and noticed that macroalgae (mostly Rhodophyta), which dominated at the cave entrance, 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 (1955) described a type of coralligenous biocoenosis developing 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 coating of ferromanganese oxides on the rocky walls of their inner reaches (Vacelet 1964). The occurrence of ferromanganese oxides in dark marine caves recalls the formation of metallic nodules in deep oceanic sediments under aphotic conditions (Pérès 1967). 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.

The clear distinction of the marine cave biocoenoses from the coralligenous was based on the dominance of sessile animals versus macroalgae (Vacelet 1959, Laborel 1960, 1961). Vacelet (1959) reported that at the cave entrance, a transitional community between the photophilic algae and the coralligenous biocoenosis (also known as 'precoralligenous') can develop. However, according to Laborel (1961) coralligenous concretions are not the most characteristic feature of marine cave communities, which are dominated by sessile animals, *Corallium rubrum* being the most typical species. Therefore, Laborel & Vacelet (1959) described two successive assemblages that develop in marine caves along a decreasing light gradient: a transitional dim-light zone, where biotic cover decreases from 100% (at the outer zone) to 50%, with the most characteristic taxa being sponges and scleractinian corals; and a completely dark zone, dominated by serpulid polychaetes, sponges and scleractinians and where biotic cover decreases to 20% or less.

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: the coralligenous biocoenosis (biocénose coralligène – C), which can often develop at the cave entrance; the semidark cave biocoenosis (biocénose des grottes semi-obscures – GSO), which – in the virtual absence of macroalgae – is dominated by sponges and anthozoans; and the biocoenosis of caves and dead-end passages in total darkness (biocénose des grottes et boyaux à obscurité totale – GO), which is characterized by sponges, serpulid polychaetes and motile crustaceans. Pérès (1967) highlighted that the coralligenous biocoenosis can develop both outside and inside marine caves, while several species of the semidark cave biocoenosis can be found as 'enclaves' in dark holes and crevices of the coralligenous formations. The presence of coralligenous assemblages at the entrance of submarine caves has been reported from several Mediterranean regions (e.g. Ballesteros 2006, Kipson et al. 2011, Teixidó et al. 2011, Gerovasileiou et al. 2017b).

Riedl (1966) studied marine caves with various 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 other taxa. Riedl's zonation scheme is typical of blind-ended caves but may not apply to marine caves with different shape. The boundaries and extent of the different zones depend on the topographic features of each cave (e.g. entrance width-to-cave length ratio, substratum inclination at the cave entrance and number of entrances), which affect light gradients and water exchange within the cave. For instance, 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. Therefore, even neighbouring marine caves could exhibit biotic heterogeneity due to their different morphology and cave-specific topographic features.

Pouliquen (1972) studied marine caves in the Marseille region and concluded that the benthic biocoenoses described from marine caves in previous studies can exhibit differences, or even be absent, according to cave typology. He distinguished three types of marine caves based on their bathymetry: 'superficial caves', partly above the sea level, where no clear patterns of biological zonation occur due to their high hydrodynamic regime; 'semi-superficial caves', located at 0 to 5 m depth, which are also characterized by high hydrodynamic forces but exhibit biological zonation shaped mainly by water movement; and 'deep caves', which are located at depths greater than 10 m, where light and hydrodynamic forces 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' 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, which often act in combination, generating isolation and oligotrophy. The transition from the semidark (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 nodules on the ceiling of the cave.

Developing some of the ideas of Harmelin et al. (1985), Bianchi & Morri (1994) postulated that beside light, hydrological confinement was the main driver of biological zonation in marine caves. The term 'confinement' relates to water renewal and the replacement of 'vital elements' (e.g. trace elements and vitamins) of marine origin, and was first introduced by Guelorget & Perthuisot (1983, 1992) for transitional coastal ecosystems (e.g. coastal lagoons). Studying 17 marine caves in Italy (Ligurian Sea, Tyrrhenian Sea, Sardinia and Sicily Channel) and four in the Maldives (Indian Ocean), Bianchi & Morri (1994) distinguished six ecological zones based on structural and functional aspects of the biotic assemblages.

Apart from the occasional attention given to biological cover, most of the above-mentioned bionomic studies provided mainly qualitative descriptions of the benthic communities in marine caves and rarely quantified spatial variability. To date, only a small number of studies have investigated marine cave benthos in a quantitative manner, using either destructive (scraped quadrats) or non-destructive (still-framed photography) 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, Gerovasileiou & Voultsiadou 2016, Gerovasileiou et al. 2017b, Sanfilippo et al. 2017, Dimarchopoulou et al. 2018, Rosso et al. 2019, Bitner & Gerovasileiou 2021). The continuous development of 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, 2017a and references therein).

Almost all the above-mentioned bionomic studies have focused on hard substratum communities, while only few studies have so far investigated macro- and meiobenthos thriving in the sediments of marine caves in France, Italy and Spain (e.g. Monteiro-Marques 1981, Bianchi & Morri 2003, Akoumianaki & Hughes 2004, Todaro et al. 2006, Navarro-Barranco et al. 2012, 2013a,b, 2014, Janssen et al. 2013, Romano et al. 2018, 2020, Bergamin et al. 2020, Pino de la Torre et al. 2020).

Environmental gradients and ecosystem functioning

The dramatic environmental gradients in Mediterranean marine caves have attracted the interest of researchers since the early stages. The disappearance of light and the effect of water movement inside caves, depending on cave geomorphology (e.g. blind-ended versus tunnels; deep versus shallow), 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 the Grotta Marina of Bergeggi, Italy (Bianchi et al. 1986, Sgorbini et al. 1988, Morri et al. 1994a), and in marine caves of Marseille region, France (Fichez 1989, 1990a,b,c, 1991a,b,c), revealed an extreme impoverishment of the food intake observed in the more confined cave sections, which was presumed to affect community composition and ecosystem functioning (trophic depletion hypothesis). However, the exploration of marine caves with internal sulphur springs in Cape Palinuro (Italy) shed light on a unique ecosystem based on microbial chemo-litho-autotrophy, resembling deep-sea hydrothermal vents (e.g. Abbiati et al. 1992, Bianchi et al. 1994, Cinelli 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 diel horizontal migrations of swarm-forming mysids and schooling fishes, 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 pivotal in order to monitor dynamics and potential changes of marine cave communities and provide evidence-based conservation.

Biodiversity

From the first pioneer taxonomic studies in Mediterranean marine caves, it became evident that they harbour several previously undescribed species. In his historical monograph, Riedl (1966) listed a total of 905 taxa, estimating that the overall diversity in Mediterranean marine caves could reach 2000 species. Many of these taxa (529 taxa belonging to 32 major groups) were recorded in marine caves of the Tyrrhenian Sea. Nearly 50 years later, updates for many taxa in Italian marine caves were provided by Cicogna et al. (2003). The study of Gerovasileiou et al. (2015a) combined information from 62 literature sources with data from primary research in 23 marine caves of the eastern Mediterranean Sea and listed 520 taxa belonging to 34 major groups. Several reviews, meta-analyses, checklists and large-scale surveys on marine cave biota have been 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), and for the whole Mediterranean Sea (Gerovasileiou & Voultsiadou 2014).

Overall diversity and regional patterns

The overview of 360 literature sources (peer-reviewed and grey literature) showed that 2369 taxa (compare to the 2000 species predicted by Riedl more than half a century ago), which belong to 58 major taxonomic groups, have been reported from 404 marine caves (mostly semi-submerged and/or shallow) in 15 Mediterranean countries. This census is based on data by Gerovasileiou (2014), Gerovasileiou & Voultsiadou (2014), Gerovasileiou et al. (2015a) and recent studies (e.g. Sanfilippo et al. 2017, Lage et al. 2018, 2019, Romano et al. 2018, 2020, Öztürk 2019, Rosso et al. 2019, Castelló et al. 2020). Taxa have been cross-checked and taxonomically updated using the World Register of Marine Species (WoRMS Editorial Board 2020) and the World Register for marine Cave Species (WoRCS) thematic database (Gerovasileiou et al. 2020). Taxa identified only at taxonomic ranks above species (e.g. genus, family) have been considered only when no other taxon of the same or lower rank was reported from other marine caves. Soft sediment thanatocoenoses have been excluded. However, in some cases data sources did not specify if species were found as living or dead specimens. All taxa reported from at least one Mediterranean marine cave have been considered. All cave zones (i.e. entrance, semidark and dark), types (i.e. marine caves proper, marine and brackish-water layers of anchialine caves, semi- and entirely submerged, blind-ended caves and tunnels), substrata (i.e. hard and soft sediments) and Mediterranean regions have been considered.

However, as expected, not all Mediterranean regions and taxonomic groups received the same research 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 (129, 88 and 52 studies, respectively). Sponges were by far the most investigated group (160 studies), followed by anthozoans (87), polychaetes (63), bryozoans (60), decapods (43), bivalves (44) and fishes (40) (Table 2). Very few studies examined microbes, planktonic taxa and miscellaneous ‘small’ groups, such as soft substratum meio- and macrofauna. The number of species per taxonomic group and marine region was positively correlated to research effort (Figure 4), expressed as both the number of studies and caves explored (Gerovasileiou & Voultsiadou 2012, 2014, this study). Research in a greater number of marine caves in different Mediterranean regions is expected to lead to an increment in the number of species known, particularly within ‘inconspicuous’ groups (Bianchi 2007).

According to the biodiversity census for Mediterranean marine caves by Gerovasileiou & Voultsiadou (2014) and this study, the highest number of taxa (both sessile and motile) in the literature has been reported from the semidark zone of marine caves (1153), followed by the cave entrance (988) and the dark zone (848). However, for 510 taxa, cave zone was not specified in the literature sources (Table 2). Macroalgae (mostly rhodophytes) dominated in terms of species richness in the entrance zone (23% of the species), while sponges dominated in the semidark and dark zones (19% and 22.4%, respectively). Bryozoans and polychaetes were also among the richest groups in all zones. A total of 438 taxa were recorded in sediments on the cave bottom and 54 taxa in the marine and brackish-water layers of anchialine caves.

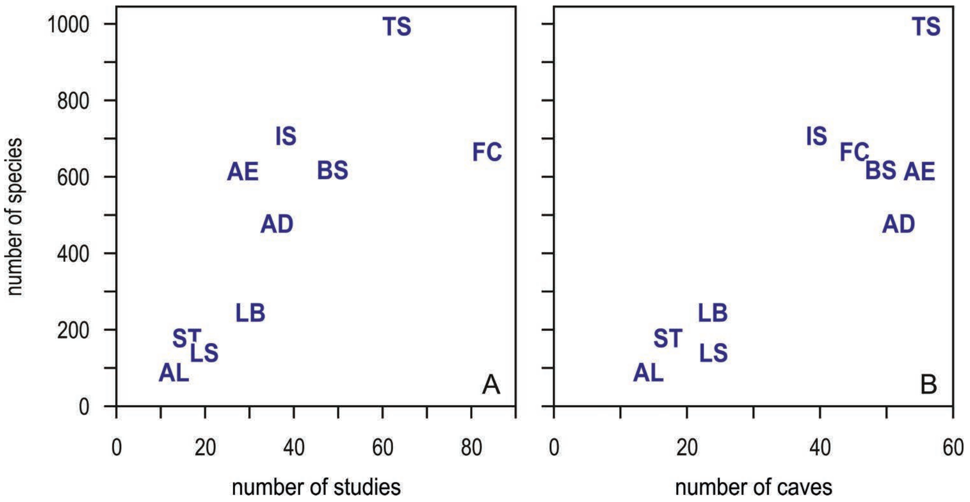

Figure 4 Relationship between cave species richness and research effort, expressed in terms of number of studies (A) and of caves investigated (B) in different Mediterranean regions. AL, Alboran Sea; BS, Balearic Sea; FC, French Coast; LS, Ligurian Sea; TS, Tyrrhenian Sea; ST, Siculo-Tunisian Strait; AD, Adriatic Sea; IS, Ionian Sea; AE, Aegean Sea; LB, Levantine Basin. Spearman's rank correlation coefficient (r_s) and probability level (p) are: $r_s=0.891$ and $p=0.001$ for A; $r_s=0.748$ and $p=0.013$ for B. Based on data from Gerovasileiou & Voultsiadou (2014), updated with recent studies.

Marine cave biota

This section provides an outline of existing knowledge (diversity patterns, frequently recorded taxa, cave-exclusive and non-indigenous species) of Mediterranean marine cave biodiversity for the main taxonomic groups (Table 2). Species are 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). Within each taxonomic group, species are listed in decreasing order by number of records. Each record represents occurrence in a different Mediterranean marine cave. All cave zones, from the entrance to the inner dark zone, have been considered.

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 the microbial mats of the famous Grotta Azzurra and Grotta Sulfurea of Cape Palinuro, 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). Microbial mats have also been 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). The cyanobacterium *Leibleinia gracilis* was abundant in the semidark zone of the Grotta del Mago, Ischia Island, Italy (Cinelli et al. 1977).

Microalgae

Many unicellular photosynthetic organisms can thrive under extremely dim light conditions and are thus able to penetrate marine caves (Riedl 1966). However, studies of microalgae in Mediterranean marine caves are extremely scarce. Mazzella et al. (1979) found 28 species of diatoms in the volcanic cave Grotta del Mago, Ischia Island, Italy, none of them being exclusive of the cave habitat.

Table 2 Number of taxa and studies on marine cave biota by taxonomic group, Mediterranean sector and cave zone.

	Mediterranean sectors										Cave zone			Number	Number	Proportion of
Taxonomic group	AL	BS	FC	LS	TS	ST	AD	IS	AE	LB	CE	SD	D	of studies	of taxa	Mediterranean diversity (%)
Bacteria					+		+	+				1	10	7	12	–
Bacillariophyceae					+							20	5	2	21	2.9
Foraminifera	+	+	+		+			+	+	+	7	8	10	17	106	17.7
Myzozoa								+				1	1	1	1	–
Ciliophora								+			11	16	15	2	20	–
Radiozoa								+			2	2	2	1	2	–
Phaeophyceae		+	+	+	+	+	+	+	+		33	2		20	35	13
Chlorophyta	+	+	+	+	+	+	+	+	+	+	27	4		26	30	15.8
Rhodophyta	+	+	+	+	+	+	+	+	+	+	169	30		34	182	27.7
Porifera	+	+	+	+	+	+	+	+	+	+	137	213	189	161	329	48.3
Hydrozoa		+	+	+	+	+	+	+	+	+	49	60	17	34	108	23.6
Scyphozoa		+					+		+		2	2	1	2	4	20
Anthozoa	+	+	+	+	+	+	+	+	+	+	24	26	25	92	53	32.1
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	2	4	8	1.6

(*Continued*)

Table 2 (*Continued*) Number of taxa and studies on marine cave biota by taxonomic group, Mediterranean sector and cave zone.

	Mediterranean sectors										Cave zone			Number	Number	Proportion of
Taxonomic group	AL	BS	FC	LS	TS	ST	AD	IS	AE	LB	CE	SD	D	of studies	of taxa	Mediterranean diversity (%)
Cirripedia			+	+	+		+	+			1	1	4	13	7	17.5
Decapoda	+	+	+	+	+	+	+	+	+	+	24	44	35	43	75	19.5
Mysida		+	+	+	+	+	+	+	+		6	6	7	22	21	20.6
Thermosbaenacea		+	+										2	2	2	33.3
Facetotecta								+						1	1	–
Tanaidacea	+		+		+		+		+			3	4	6	6	14
Pentastomida								+					1	1	1	–
Isopoda	+		+		+		+	+	+	+	2	7	6	12	26	15.8
Leptostraca		+											1	2	1	16.7
Amphipoda	+	+	+	+	+				+		26	59	30	19	83	18.5
Cumacea	+		+		+							2	5	6	6	6.1
Branchiopoda								+			3	4	3	1	4	–
Pycnogonida			+		+						3	15	2	4	15	33.3
Acari					+									2	5	–
Insecta (marine)								+			1	1		1	1	0.4
Oligochaeta					+									4	2	–
Polychaeta	+	+	+	+	+	+	+	+	+	+	86	186	113	63	262	23.4
Sipuncula			+		+		+		+		2	5	3	9	6	16.7
Echiura		+		+			+		+		1		1	4	1	16.7
Polyplacophora			+		+						5			7	7	22.6
Gastropoda	+	+	+	+	+	+	+	+	+	+	68	76	39	41	139	8.9
Bivalvia	+	+	+	+	+	+	+	+	+	+	31	41	30	48	93	23.3
Caudofoveata					+							1		1	1	3.4

(*Continued*)

Table 2 (*Continued*) Number of taxa and studies on marine cave biota by taxonomic group, Mediterranean sector and cave zone.

	Mediterranean sectors										Cave zone					
Taxonomic group	AL	BS	FC	LS	TS	ST	AD	IS	AE	LB	CE	SD	D	Number of studies	Number of taxa	Proportion of Mediterranean diversity (%)
Cephalopoda				+			+		+		3	2		4	3	4.6
Tardigrada			+		+		+	+					1	3	31	40.3
Bryozoa	+	+	+	+	+	+	+	+	+	+	121	168	132	66	228	40.9
Brachiopoda	+	+	+	+		+	+		+	+		7	8	22	10	71.4
Phoronida									+		1			1	1	20
Chaetognatha		+	+					+			1	1	5	3	5	25
Pterobranchia			+										1	1	1	20
Echinodermata		+	+	+	+	+	+	+	+	+	17	21	17	31	36	23.4
Tunicata	+	+	+		+	+	+	+	+	+	24	24	13	37	45	19.7
Pisces	+	+	+	+	+	+	+	+	+	+	45	46	29	40	112	17.2
Mammalia	+							+	+	+	1	1	1		1	4.3
Number of studies	14	51	88	21	70	18	38	41	33	33				360		
Number of caves	15	61	48	25	59	18	54	41	58	25						
Number of taxa	92	620	671	144	1022	181	481	713	617	260	988	1153	848		2369	13.9%

Source: Updated from Gerovasileiou (2014) and Gerovasileiou & Voultsiadou (2014) with recent data.

Note: 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) and Rosso & Di Martino (2016) for bryozoans.

Abbreviations: AL, Alboran Sea; BS, Balearic Sea; FC, French Coast; LS, Ligurian Sea; TS, Tyrrhenian Sea; ST, Siculo-Tunisian Strait; AD, Adriatic Sea; IS, Ionian Sea; AE, Aegean Sea; LB, Levantine Basin; CE, Cave entrance zone; SD, Semidark cave zone; D, Dark cave zone.

The most common species included *Biddulphia biddulphiana*, *Amphora bigibba*, *Grammatophora serpentina*, *Licmophora gracilis*, *L. abbreviata*, *Navicula ramosissima* and *Triceratium repletum*. A number of species, such as *Cocconeis scutellum*, *Grammatophora marina* and *Rhabdonema adriaticum*, were also present in the innermost and totally dark zone. Because photosynthesis should be inhibited in the dark, it might be supposed that they were resting stages rather than active organisms; however, there are examples of cave diatoms that are myxotrophic or even heterotrophic (Lewin & Lewin 1967, Armstrong et al. 2000, Abdullin & Bagmet 2016).

Macroalgae

Macroalgae can be very abundant at the entrance zone of marine caves (Figure 5A), and in some cases, sciaphilic species penetrate further inside semidark cave sections, though with low cover (Riedl 1966, Cinelli et al. 1977, Bianchi 2003, Alongi et al. 2012, Gerovasileiou et al. 2017b, Taşkın & Akçalı 2019). A considerable number of macroalgal taxa have been reported from Mediterranean marine caves, specifically 30 Chlorophyta, 35 Phaeophyceae and 182 Rhodophyta. The most frequently reported species (all in >10 caves) were the chlorophytes *Palmophyllum crassum* (Figure 5A), *Flabellia petiolata*, *Halimeda tuna* and *Valonia macrophysa*; the phaeophytes *Halopteris filicina* and *Dictyota dichotoma*; and the rhodophytes *Peyssonnelia squamaria*, *Lithophyllum stictiforme*, *Peyssonnelia rubra*, *Plocamium cartilagineum* and *Sphaerococcus coronopifolius*. The crustose rhodophyte *Hildenbrandia rubra* was the macroalgal species that penetrated furthest in the Grotta del Mago, Ischia Islands, Italy (Cinelli et al. 1977). The same species is also very abundant in caves of Crete, Greece (V. Gerovasileiou, unpublished data).

Foraminiferans

The most widely reported foraminiferan in Mediterranean marine caves is *Miniacina miniacea* (in >20 caves), which is a sessile benthic species, clearly visible to the naked eye (Figure 5B). It can cover up to 1% of the total biotic cover (Balduzzi & Cattaneo 1985, Dimarchopoulou et al. 2018) and – together with other taxa – may contribute to bioconstructions (Ballesteros 2006, Sanfilippo et al. 2015). There are very few studies, providing scattered information, of benthic (e.g. Riedl 1966, Rosso et al. 2019) or planktonic foraminiferans (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, only 14 foraminiferan species were reported (Gerovasileiou & Voultsiadou 2014). However, recent detailed studies of benthic foraminiferans in two marine caves of Sardinia, Italy (Bergamin et al. 2018, Romano et al. 2018, 2020, E. Romano, personal communication) yielded 131 taxa in cave sediments, of which 101 were represented by living individuals. Based on these updates, the foraminiferan diversity of Mediterranean marine caves should be approximately 106 taxa (considering only living species).

Sponges

Porifera is one of the most abundant and species-rich phyla in Mediterranean marine caves (Sarà 1962, Pouliquen 1972, Corriero et al. 2000, Cadeddu 2012, 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 one 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 (Vacelet 1994, Pisera & Gerovasileiou 2021). 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* – Figure 5B), and >30 cave-exclusives (Gerovasileiou & Voultsiadou 2012, Grenier et al. 2018). In addition, several deep-sea species were found in dark marine caves, such as the carnivorous cladhorizid *Lycopodina hypogea* and the

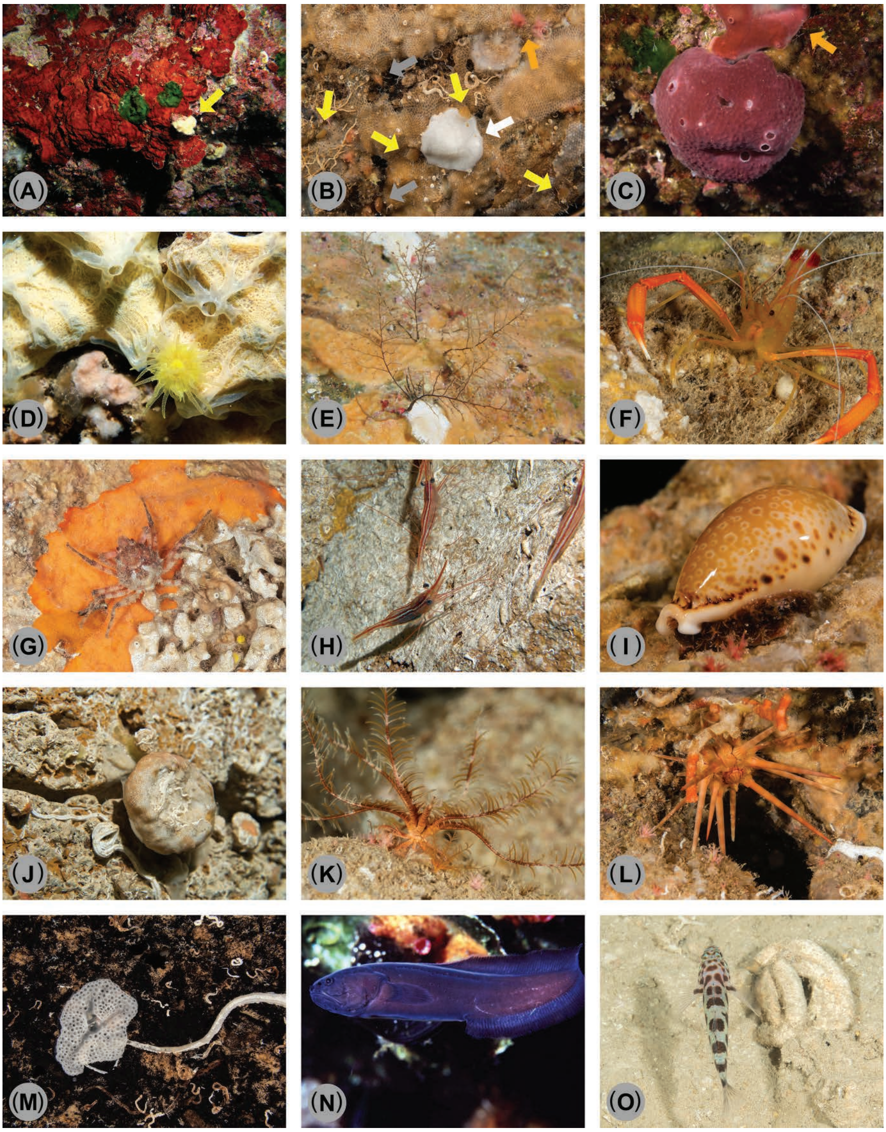

Figure 5 Characteristic species of Mediterranean marine caves: (A) the rhodophyte *Peyssonnelia rosa-marina*, the chlorophyte *Palmophyllum crassum* and nodules of the bryozoan *Rhynchozoon neapolitanum* (yellow arrow); (B) the calcareous sponge *Petrobiona massiliana* (white arrow), the foraminiferan *Miniacina miniacea* (orange arrow) and the brachiopods *Argyrotheca cuneata* (grey arrows) and *Joania cordata* (yellow arrows) on a cave wall with bryozoan encrustations; (C) the demosponges *Ircinia variabilis* and *Petrosia ficiformis* (orange arrow) and the chlorophyte *Palmophyllum crassum*; (D) the scleractinian coral *Leptopsammia pruvoti* and the demosponge *Hexadella racovitzai*; (E) hydrozoans (*Eudendrium* sp.) together with bryozoan encrustations on the walls of a submerged tunnel; (F) the shrimp *Stenopus spinosus*; (G) the spider crab *Herbstia condyliata*; (H) *Plesionika narval* shrimps on the walls of a dark cave; (I) the gastropod *Naria spurca* and the foraminiferan *Miniacina miniacea* in a semidark cave; (J) fungiform nodule formed mainly by the bryozoan *Hippaliosina depressa*; (K) the crinoid *Antedon mediterranea*, (L) the sea urchin *Stylocidaris affinis* and the bryozoan *Myriapora truncata*; (M) the didemnid ascidian *Lissoclinum perforatum* and serpulid tubes on a dark cave wall; (N) the cave-dwelling fish *Grammonus ater* in a dark cave; (O) the leopard-spotted goby *Thorogobius ephippiatus* over a muddy cave bottom. Photos by V. Gerovasileiou (A), T. Dailianis (B–M and O) and Donat Petricioli (N).

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* (Figure 5C), *Spirastrella cunctatrix*, *Ircinia variabilis* (Figure 5C), *Phorbas tenacior*, *Crambe crambe*, *Chondrosia reniformis*, *Axinella damicornis*, *Spongia virgultosa*, *Acanthella acuta*, *Penares euastrum*, *Terpios gelatinosa*, *Aaptos aaptos*, *Diplastrella bistellata*, *Haliclona mucosa*, *Erylus discophorus*, *Aplysilla sulfurea*, *Haliclona sarai*, *Ircinia oros*, *Cliona viridis*, *Penares helleri* and *Spongia officinalis*; the calcareous sponges *Clathrina coriacea* and *Petrobiona 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 region). 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 165 cnidarian species have been reported from Mediterranean marine caves (53 Anthozoa, 108 Hydrozoa and 4 Scyphozoa). Anthozoans represent one of the most abundant and widespread taxa in marine caves, where they can form dense facies, especially on the ceilings and walls of the semidark cave zone. Examples include the scleractinians *Leptopsammia pruvoti* (Figure 5D), *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 sections; the red coral *Corallium rubrum*, which is more common in the north-western Mediterranean; and *Parazoanthus axinellae*, which can be abundant in cave entrances or in semidark tunnels with high hydrodynamic forces (Pérès 1967, Zibrowius 1978, Gili & Ballesteros 1991, Gerovasileiou et al. 2015a). In addition, gorgonian facies (e.g. *Eunicella cavolini* and *Paramuricea clavata*) can develop at cave entrances, mostly in the western Mediterranean. The most common sea anemone in marine caves, *Cerianthus membranaceus*, is often found in the sediment of cave bottoms, in both semidark and dark zones. Hydroids prefer cave sections with good water circulation, such as entrances or tunnels (Figure 5E) (e.g. Riedl 1959b, Boero 1985, 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, eight non-indigenous and cryptogenic hydroids have been reported in caves (Gerovasileiou et al. 2016b), mostly in the Levantine Sea (Morri et al. 2009), with the circumtropical *Clytia linearis* being the most widespread throughout the Mediterranean.

Annelids

While oligochaetes have been rarely found in Mediterranean marine caves (Akoumianaki & Hughes 2004), polychaetes have been recorded in high number (262 species), mostly on hard substrata. 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 substrata (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 other 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. 2013a, 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 form dense aggregates. 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 the Grotta Azzurra of Cape Palinuro, Italy). However, the small number of studies on soft substratum macrobenthos does not allow diversity patterns to be generalized.

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 2). Due to the scarcity of studies on soft substratum macro- and meiofauna and zooplankton assemblages, there is little information about their diversity in this 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 375 arthropods from several taxonomic groups, mostly crustaceans, have been reported so far from Mediterranean marine and anchialine caves (Table 2). The groups with the highest number of species are Copepoda (113), Amphipoda (83), Decapoda (75), Isopoda (26), Mysida (21) and Pycnogonida (15), with all other groups comprising less than 10 taxa. The most frequently reported species (in >10 caves) were the decapods *Stenopus spinosus* (Figure 5F), *Herbstia condyliata* (Figure 5G), *Palinurus elephas*, *Palaemon serratus*, *Dromia personata*, *Galathea strigosa*, *Plesionika narval* (Figure 5H) and *Scyllarus arctus*, and the mysids *Hemimysis margalefi*, *H. speluncola* and *Siriella jaltensis*. These species move into and out of caves, with the first two mysids forming swarms, thus playing an important role in the functioning of the marine cave ecosystem. Marine cave decapods have been especially studied by Gili & Macpherson (1987), who reported 11 species from Mallorca Island, Spain, and by Manconi & Pessani (2003), who reported 24 species from 21 Italian marine caves. The high number of copepod species in Mediterranean caves derives from one study on zooplankton assemblages of Grotta di Ciolo, Italy (Moscatello & Belmonte 2007), and one study on soft substratum 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 high 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, the Balearic Islands and south France (e.g. Pretus 1990, Fransen 1991, Jaume & Boxshall 1996, Jaume 1997, Jaume et al. 1999, Wagner & Chevaldonné 2020). The molecular study of mysids in several marine caves from different Mediterranean regions by Rastorgueff et al. (2014) revealed at least four cryptic *Hemimysis* taxa still undescribed. 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. Seven non-indigenous and cryptogenic crustaceans have been found in Mediterranean marine caves (Gerovasileiou et al. 2016b), with the Indo-Pacific shrimp *Urocaridella pulchella* being the most recent addition, having been reported from Aegean and Levantine caves (Digenis et al. 2021).

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 243 species, mostly gastropods (139) and bivalves (93). Other classes are represented with fewer than 10 species (seven Polyplacophora, three Cephalopoda and one 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* and the spiny file clam *Lima lima* (all in >10 caves). The gastropods *Naria spurca* (Figure 5I) and *Luria lurida*, included in Annex II (List of endangered or threatened species) of the Bern Convention and the SPA/BD Protocol of the Barcelona Convention, are more commonly observed in caves than elsewhere (Bianchi 2003). Radolović et al. (2015) reported unusually high abundance of the gastropod *Homalopoma sanguineum* in the Y-Cave of Croatia. In the dark part of caves with terminal air domes, the deep circalittoral bivalve *Neopycnodonte cochlear* was seen forming thick encrustations on rocky walls just below the water surface in marine caves of Salento and the Sorrentine Peninsula (Italy) and of Croatia (C.N. Bianchi, personal observations in 1979, Cattaneo-Vietti & Russo 1987, Arko-Pijevac et al. 2001, Novosel et al. 2002, Onorato et al. 2003). Some mollusc species were first described from marine caves, such as the gastropods *Hyalogyra zibrowii*, *Skeneoides digeronimoi* and *Ocenebra vazzanai*, and the bivalves *Asperarca magdalenae*, *Neolepton discriminatum* and *Lucinoma spelaeum* (Warén et al. 1997, La Perna 1998, 1999, Palazzi & Villari 2001, Crocetta et al. 2020). Nevertheless, it remains unknown if these species are exclusive cave dwellers or if they simply prefer cryptobiotic and deep-water environments which are not easily sampled (Crocetta et al. 2020). A total of 15 non-indigenous and cryptogenic molluscs (eight bivalves and seven gastropods) were recorded in Mediterranean marine caves, mostly in 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 & Russo 2013, Crocetta et al. 2013a,b, Gerovasileiou et al. 2016b).

Brachiopods

Brachiopoda exhibit a particular preference for marine caves, often developing in large populations on the ceiling of the dark sections (Logan et al. 2004, Bitner & Gerovasileiou 2021). Out of the 14 brachiopods occurring in the Mediterranean Sea, nine to ten (64–71%) have been found in marine caves. The most frequently recorded species are *Joania cordata* (Figure 5B), *Argyrotheca cuneata* (Figure 5B), *Novocrania anomala* (although some records could actually belong to the congeneric species *N. turbinata* – see Bitner & Gerovasileiou 2021), *Argyrotheca cistellula*, *Tethyrhynchia mediterranea* and *Megathiris detruncata*. The rhynchonellid *Tethyrhynchia mediterranea* was first described from marine caves of southern France and Tunisia (Logan & Zibrowius 1994) and has not been recorded from other habitats to date. *Novocrania anomala* can be found in considerable numbers, cemented on dark cave walls and ceilings (Logan et al. 2004, Radolović et al. 2015, Rosso et al. 2019). Several brachiopod shells can be found in sediments of the cave bottom as thanatocoenoses, having detached from the cave ceiling (Taddei Ruggiero 1994, Bergamin et al. 2020, Pino de la Torre et al. 2020).

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 semidark and dark cave biocoenoses, where several encrusting taxa (e.g. *Onychocella marioni* and *Hippaliosina depressa*) may develop multilayered structures (Figure 5J) (Harmelin 1985, 2000, Harmelin et al. 1985, 2003, Rosso et al. 2013a, 2015, 2019, 2020b). 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* and *Schizoretepora serratimargo*; and the cyclostomes *Crisia sigmoidea*, *Disporella hispida*, *Diplosolen obelius*, *Harmelinopora indistincta*, *Annectocyma major* and *Crisia pyrula*. Several bryozoan species were first described from Mediterranean marine caves (e.g. Hayward 1974, Silén & Harmelin 1976, Harmelin et al. 2007, Rosso et al. 2020a). According to Harmelin (1986), the bryozoan fauna of dark caves exhibits affinities with that of other crevicular microhabitats (e.g. coralligenous concretions), undersides of small hard substrata and deep-sea habitats. Rosso et al. (2013a) 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. Non-indigenous taxa and new species with Indo-Pacific affinities have been recorded in marine caves of Lebanon (Harmelin et al. 2007, 2009, 2014a,b).

Echinoderms

The echinoderm fauna of Mediterranean marine caves is represented by 36 species in total. The most frequently reported taxa (>10 caves) are the sea urchin *Arbacia lixula*, which can occasionally enter shallow caves, and the brittle star *Ophiothrix fragilis*. Echinoderms are never abundant in caves except for some ophiurids (e.g. *Amphiura chiajei* and *Ophioderma longicaudum*) and, to a lesser extent, asteroids (Tortonese 1978). The crinoid *Antedon mediterranea* (Figure 5K) is abundant in the Grotta Azzurra of Cape Palinuro, Italy (Bianchi et al. 1994, Cinelli et al. 1994). The same species and the sea urchin *Stylocidaris affinis* (Figure 5L) have been also observed in relatively high abundance in some marine caves of Crete, Greece (V. Gerovasileiou, personal observation).

Tunicates

A total of 45 tunicate species have been recorded in Mediterranean marine caves, mostly Ascidiacea, except for two undetermined salps that had drifted in from the 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 semidark cave biocoenosis by Pérès (1967). Didemnids can be also common in eastern Mediterranean marine caves (Figure 5M) (V. Gerovasileiou, unpublished data). The rare species *Rhodosoma callense*, which has the shape of a box with an articulated lid, was found and redescribed, after its first description in the nineteenth century, in two marine caves of Marseille region (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. 2016b). Certain colonial species (e.g. *Clavelina* spp.) can locally form patches (Bianchi 2003).

Fishes

Mediterranean marine caves are used as shelters by several fish species (Riedl 1966, Bussotti et al. 2002, 2003, 2015, 2017, Bussotti & Guidetti 2009, Gerovasileiou & Voultsiadou 2014, Gerovasileiou et al. 2015a,b, Bilecenoğlu 2019); juveniles, in particular, find refuge from predators (Balduzzi et al. 1980). A total of 112 fish species have been reported from different sections 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* (Figure 5N) and *Didogobius splechtnai*; (2) species associated with cryptic habitats (e.g. crevices and fissures), also frequently found in caves, such as *Apogon imberbis*, *Conger conger*, *Corcyrogobius liechtensteini*, *Epinephelus marginatus*, *Scorpaena* spp. (*S. notata* and *S. porcus* are more common in the western Mediterranean, while *S. maderensis* is more common in the eastern basin), *Sciaena umbra*, *Serranus cabrilla*, *S. scriba*, *Phycis phycis* and *Thorogobius ephippiatus* (Figure 5O); and (3) several nectobenthic species inhabiting rocky reefs that can occasionally be found in caves, but usually close to the entrance (e.g. *Coris julis*, *Diplodus* spp., *Sarpa salpa* and *Symphodus* spp.). The cardinal fish *Apogon imberbis* is by far the most frequently reported and abundant species in marine caves, contributing to the mitigation of trophic depletion through its diel inside–outside migrations. One of the most recent additions to the Mediterranean cave fish fauna is the deep-water Messina rockfish *Scorpaenodes arenai* that was photographed for the first time by a scuba diver in a submerged cave (26–31 m) of Zakynthos Island, Ionian Sea, Greece (Tsiamis et al. 2015), and non-indigenous species of Indo-Pacific origin (e.g. *Sargocentron rubrum*, *Pempheris rhomboidea* and *Pterois miles*) in caves of the eastern Mediterranean Sea (Gerovasileiou et al. 2016b, and unpublished data by V. Gerovasileiou and C.N. Bianchi).

Birds and mammals

Some seabirds and rock pigeons (*Columba livia*) that inhabit the rocky coasts often find refuge, especially at the time of nesting, in the subaerial part of large semi-submerged caves, but none can be considered as typical (Cattaneo & Pastorino 1974; Galli & Spanò 2003, V. Gerovasileiou, personal observations).

Among mammals, the Mediterranean monk seal *Monachus monachus* is one of the most emblematic species to use this habitat (Mo 2003). There is historical evidence of the use of caves by this species: in Italy, for instance, many traditional marine cave names, such as ‘Grotta delle Sirene’ (= Mermaids Cave) or ‘Grotta del Bue Marino’ (= Sea Ox Cave), derive from the (past) occurrence of monk seals there. However, the bibliography of these last two centuries indicates a progressive increase in the 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, give birth and nurse pups, has been an adaptation to the intense human persecution to which it has been exposed since classical antiquity (Voultsiadou et al. 2013). 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 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 and a chamber with a wide beach or with a highly inclined beach (Gücü et al. 2004, Karamanlidis et al. 2004, Dendrinos et al. 2007).

Some bat species (e.g. *Miniopterus schreibersii*, *Myotis blythi*, *Tadarida teniotis*) find refuge in the subaerial part of semi-submerged caves and tunnels, often in large populations (Galli & Spanò 2003, Mačić et al. 2019 and V. Gerovasileiou, personal observation).

Bionomy

Bionomic framing and heterogeneity

Environmental gradients in marine caves are dramatic (Morri et al. 1994a): within a few metres, there are variations of light, water movement and trophic input, which, in the external environment, can take place within tens or even hundreds of metres (Sarà 1978, Bianchi 1994). These environmental

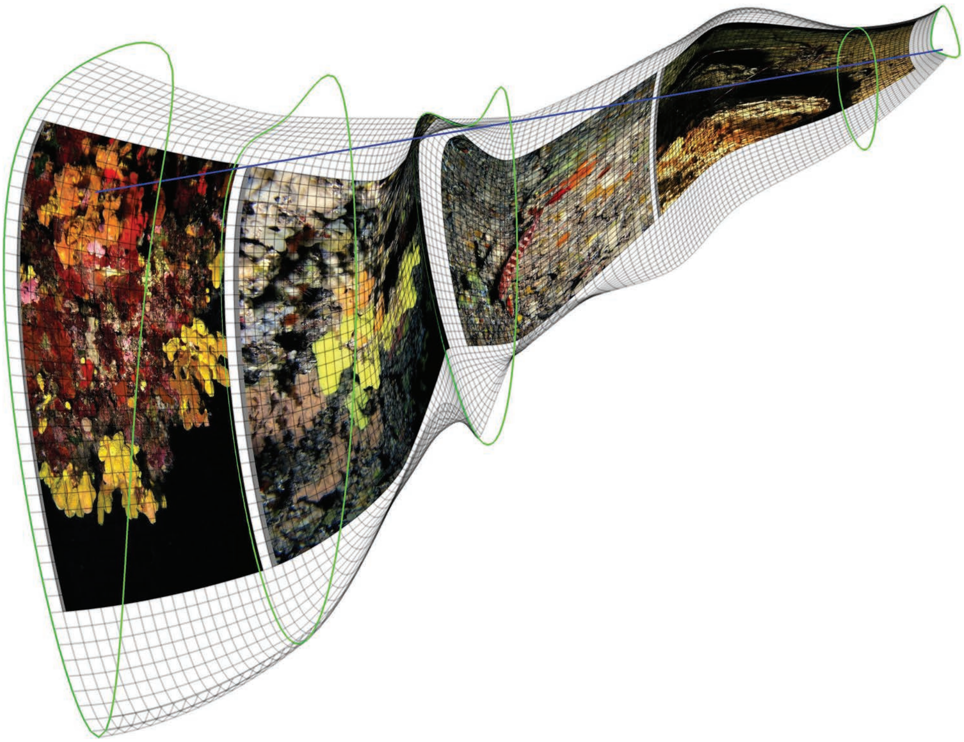

Figure 6 Ecological zonation in a blind-ended cave (24–40 m depth, Agios Vasilios Cave, Lesvos Island, Greece), depicted on a three-dimensional model. Representative images of different communities are superimposed on the cave model. From left to right, the coralligenous biocoenosis of the cave entrance is gradually replaced by the intermediate, animal-dominated semidark 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. (2017b), Sanfilippo et al. (2017), Rosso et al. (2019), and Bitner & Gerovasileiou (2021).

gradients generate a marked zonation of cave communities (Figure 6), and thus, species are not distributed homogeneously inside caves, but generally prefer distinct sections (Bianchi et al. 1996, Bianchi & Morri 1999).

In addition to the general patterns and trends of 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 pattern, 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, but might be also due to stochastic biological patchiness (Riedl 1966, Balduzzi et al. 1989, Benedetti-Cecchi et al. 1997, Martí et al. 2004a, Bussotti et al. 2006, Gerovasileiou et al. 2013, 2017b, Sempere-Valverde et al. 2019). The presence of microhabitats 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 peculiar species (Bussotti et al. 2006, Gerovasileiou et al. 2017a).

As the first ecological and bionomic studies in Mediterranean marine caves took place mostly in the north-western Mediterranean, 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 heterogeneity, with several taxa having a restricted distribution range or being common in some regions but absent from others (Gerovasileiou & Voultsiadou 2012, Bussotti et al. 2015, Gerovasileiou et al. 2015a).

The biotic zones of Riedl

Riedl (1959b, 1966) distinguished six biotic zones, based on species replacement across the outside-inside gradient of blind-ended caves (Figure 7):

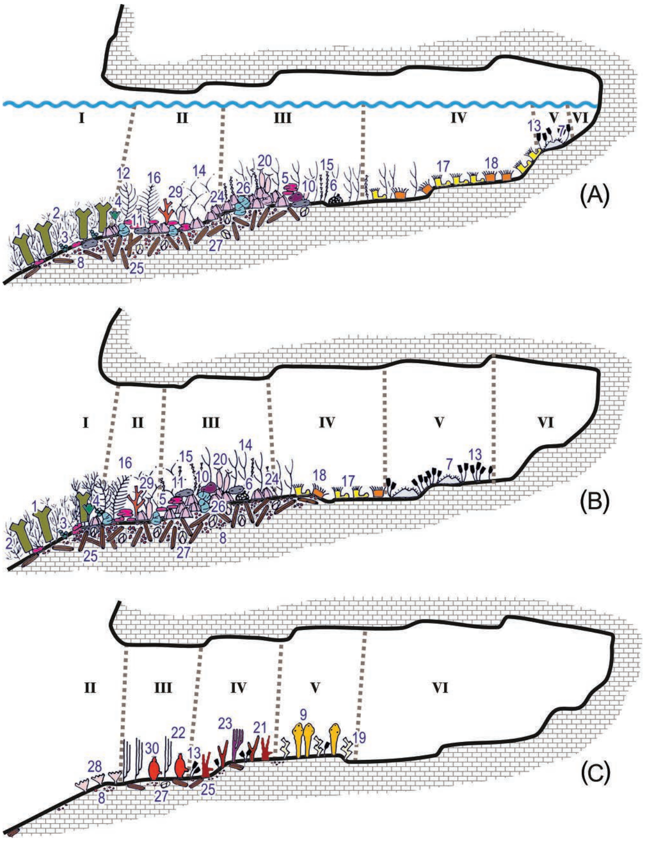

Figure 7 Biotic zones in semi-submerged caves (A), in infralittoral (B) and circalittoral (C) submerged caves according to Riedl (1966). The inner zones can occur close to the cave entrance as the depth increases. I: algal dominated zone, II: entrance zone, III: anterior zone, IV: central zone, V: posterior zone and VI: 'empty quarter'. For simplicity and graphical clarity, organisms have been schematically illustrated only on the cave floor, but walls and ceilings are also colonized: 1 *Dictyopteris*; 2 *Cystoseira*; 3 *Halimeda*; 4 *Flabellia*; 5 encrusting Rhodophyta; 6 *Clathrina*; 7 *Petrobiona*; 8 *Cliona*; 9 *Axinella*; 10 *Petrosia*; 11 *Ircinia*; 12 *Pennaria*; 13 *Campanularia*; 14 *Eudendrium*; 15 *Dynamena*; 16 *Aglaophenia*; 17 *Parazoanthus*; 18 Dendrophylliidae; 19 other Scleractinia; 20 *Cornularia*; 21 *Corallium*; 22 *Eunicella*; 23 *Paramuricea*; 24 Balanidae; 25 *Lithophaga*; 26 *Ostrea*; 27 *Rocellaria*; 28 *Reteporella*; 29 *Myriapora*; and 30 *Halocynthia*. Redrawn and modified from Riedl (1966).

(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),

(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 inside. 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 substratum. In the posterior zone, under complete darkness and calm waters, the inclination of the substratum (and hence the sedimentation) constitutes the most important factor. Finally, the 'empty quarter' (Figure 8) 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 possible freshwater infiltrations.

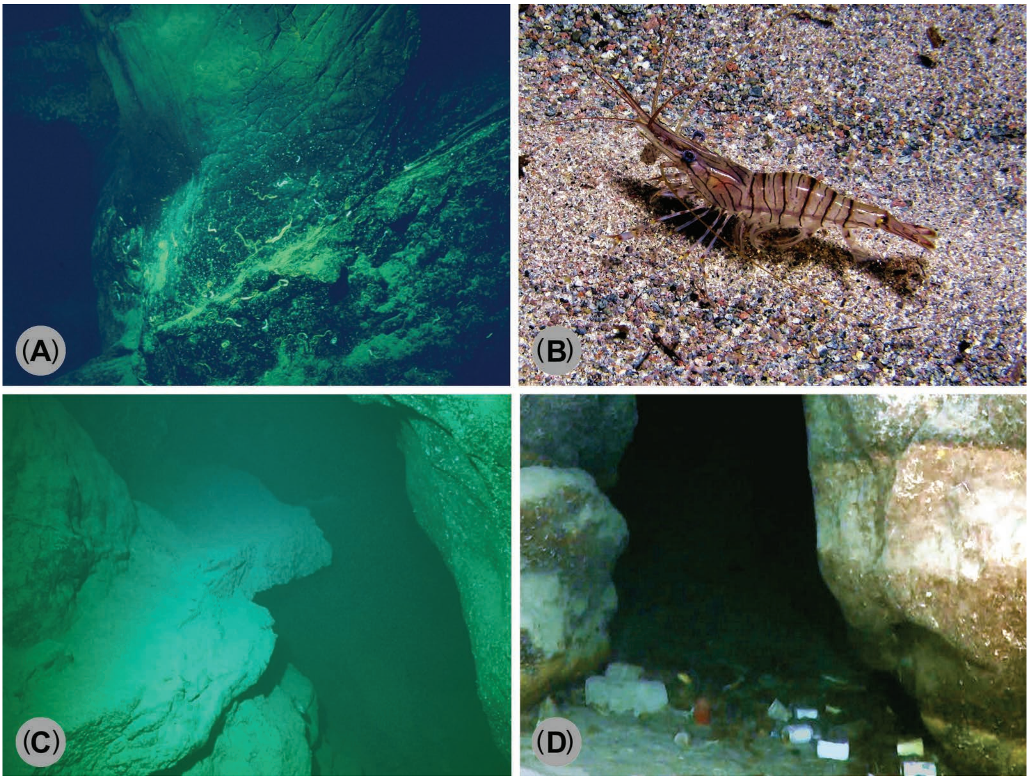

Figure 8 Aspects of the so-called leere Viertel (= empty quarter), the farthest reach of dark caves. (A) Layer of black metallic oxides and scanty serpulids on a rock wall; (B) the shrimp *Palaemon serratus* is one of the few representatives of the motile fauna; (C) the deposit of fine sediment on subhorizontal rocks hampers the settlement of sessile organisms; (D) lack of water movement may favour the accumulation of anthropogenic litter. Photos by C.N. Bianchi (A, C, D) and V. Gerovasileiou (B).

Comparing different marine caves, three main aspects were considered important in determining the zonation of the biotic zones: depth, size and shape of the cave. As for depth, deep-water caves exhibit a marked decrease in flora and fauna, with fauna being concentrated 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 wide and morphologically complex caves with narrow entrance, while it may even be absent in small caves.

However, according to Riedl, the most important factor for the distribution of the biota is the shape of the caves. In tunnel-shaped caves, where there is constant water movement and light can be very variable, it is difficult to identify a clear zonation pattern and some zones can be absent. In addition, Riedl observed that benthic assemblages similar to those of caves can also be found outside, under roofs and overhangs, suggesting a pivotal role for light.

The cave biocoenoses of Pérès & Picard

Due to the great influence of the French school on Mediterranean marine ecologists, the model of cave zonation by Pérès & Picard (1964) has been the most widely followed and accepted to date. Knowledge about the composition and structure of the two basic cave biocoenoses – the semidark cave biocoenosis or GSO (from the French 'grotte semi-obscure') and the dark cave biocenosis or GO (from the French 'grotte obscure') – has been completed and updated thanks to current data from different Mediterranean regions.

The semidark cave biocoenosis

The semidark cave biocoenosis is typically found at (or in proximity to) the entrance of caves and even under caverns and overhangs that, topographically speaking, would not be characterized as true caves. The distinction of the GSO biocoenosis from that of the coralligenous, to which it was first assimilated, 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 some encrusting rhodophytes) may occur in certain caves.

Sponges form distinctive facies in semidark caves (Figure 9A–C), where they are the most species-rich group (Vacelet 1994). In semidark caves, the most frequently recorded sponge species, ordered according to the decreasing number of records, are *Agelas oroides*, *Petrosia ficiformis*, *Spirastrella cunctatrix*, *Chondrosia reniformis* and *Phorbas tenacior* (Gerovasileiou & Voultsiadou 2012). Some sponges (e.g. *Petrosia ficiformis*) can be often discoloured due to effect of reduced light on their associated cyanobacteria. The sponge *Aplysina cavernicola* has also been described as a typical species of this biocoenosis in the north-western Mediterranean basin (Vacelet 1959), although the distinction from the closely related, photophilic species *A. aerophoba* has been questioned (Voultsiadou-Koukoura 1987). 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 semidark cave biocoenosis (Figure 9D–F), mostly on ceilings and overhangs (Pérès 1967, Zibrowius 1978): (1) facies with scleractinians, such as *Leptopsammia pruvoti*, *Madracis pharensis* (more common in the eastern Mediterranean), *Hoplangia durotrix*, *Polycyathus muellerae*, *Caryophyllia inornata* and *Astroides calycularis* (mostly in southern sectors of the western Mediterranean); (2) facies with the red coral *Corallium rubrum*, found also in shallow water in the north-western Mediterranean Sea, but only deeper (below 50 m) in the north-eastern basin; and (3) facies with *Parazoanthus axinellae*, which can be found close to the entrance or in semidark tunnels with high hydrodynamics (more common in the western Mediterranean Sea and the Adriatic Sea). Facies with erect bryozoans (e.g. *Adeonella* spp. and *Reteporella* spp.) may also develop within this biocoenosis (Pérès 1967, Ros et al. 1985).

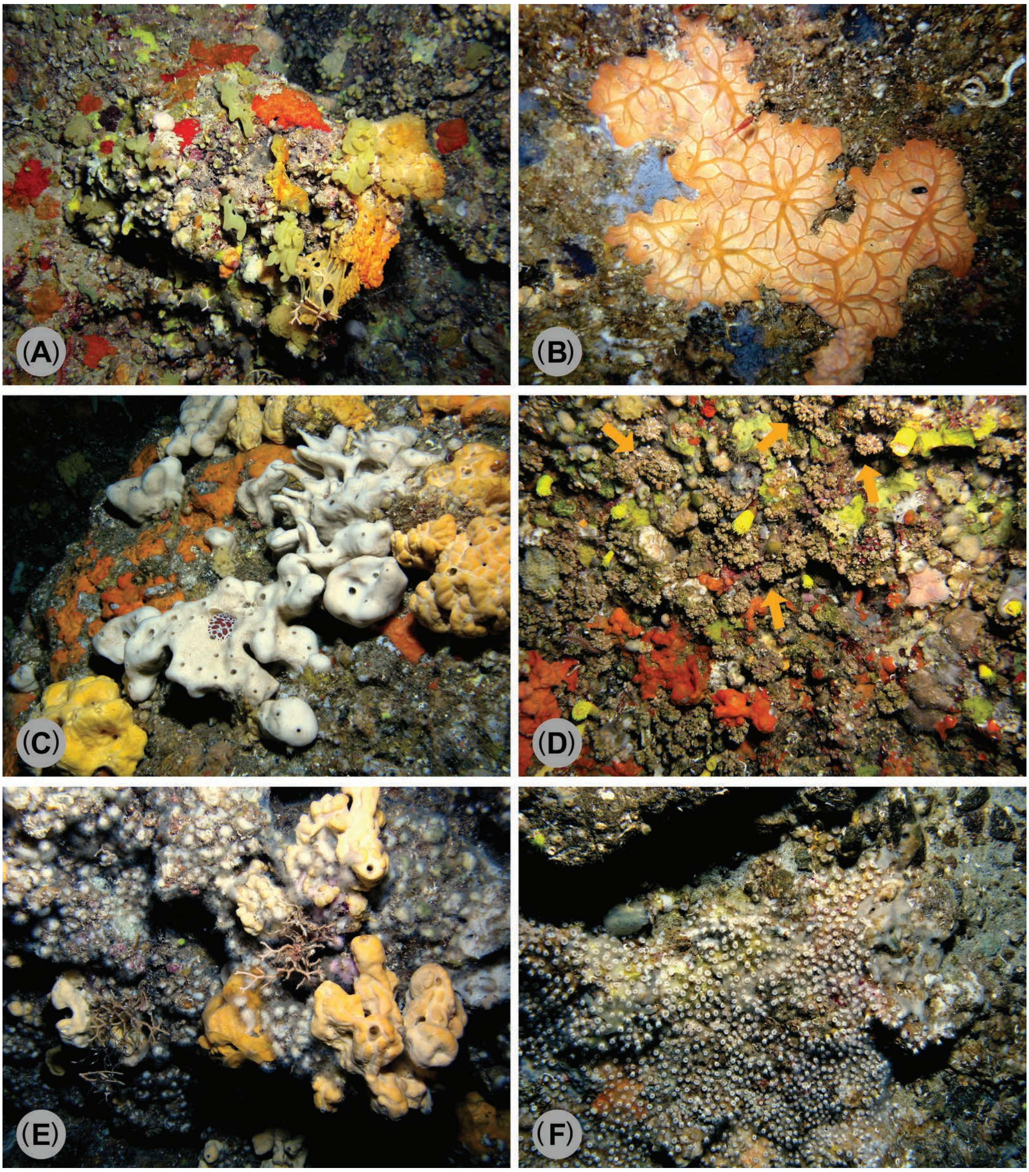

Figure 9 Typical aspects of the semidark cave biocoenosis dominated by sponges (A–C) and anthozoans (D–F): (A) *Oscarella* spp. and encrusting sponges; (B) *Spirastrella cuncatrix* (red) and *Phorbas tenacior* (pale blue) crusts; (C) discoloured *Petrosia ficiformis* (white) preyed upon by the nudibranch *Peltodoris atromaculata*, *Agelas oroides* (massive orange) and *Spirastrella cunctatrix* (orange-red); (D) facies of the scleractinian corals *Hoplangia durotrix* (orange arrows) and *Leptopsammia pruvoti* (yellow corals); (E) facies of the scleractinian *Madracis pharensis*, *Agelas oroides* and the erect bryozoan *Adeonella pallasii*; (F) facies of the scleractinian *Polycyathus muellerae*. Photos by V. Gerovasileiou.

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, in very shallow-water caves, 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.).

The dark cave biocoenosis

The dark cave biocoenosis develops in the inner sections of blind-ended caves. The shift from the semidark to the dark cave biocoenosis is evidenced through a sharp decrease in biotic cover, species richness, biomass and three-dimensional complexity (Pérès 1967). However, Harmelin et al. (1985) observed that in tunnel-shaped caves with constant water movement, biotic cover can reach 100% even in the totally dark zone (Figure 10).

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 often develop in this transitional zone (Harmelin 1985, Harmelin et al. 1985), although in some cases, they are also present in the dark cave biocoenosis (Balduzzi et al. 1989, Rosso et al. 2019).

The rock in dark cave sections is usually sparsely colonized by sponges, serpulid polychaetes, bryozoans and brachiopods (Figure 11A–D) (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) sponge *Oopsacas minuta*, which has been reported from caves of Marseille region and Croatia (Harmelin et al. 1985, Vacelet et al. 1994, Bakran-Petricioli et al. 2007). Serpulid polychaetes are among the dominant taxa in the dark cave biocoenosis, the most typical species being *Filogranula annulata*, *Janita fimbriata*, *Metavermilia multicristata*, *Serpula cavernicola*, *Spiraserpula massiliensis* and *Vermiliopsis monodiscus* (Zibrowius 1968, Sanfilippo & Mòllica 2000, Bianchi & Sanfilippo 2003). Although not exclusive to caves, the serpulid *Protula tubularia* often forms aggregates of several tubes (Figure 11C–D). The most typical, although not always abundant, bryozoans in dark caves are *Desmeplagioecia violacea*, *Ellisina gautieri*, *Glabrilaria pedunculata*, *Harmelinopora indistincta*, *Liripora violacea* and *Setosella cavernicola* (Harmelin 1969, 1985, 1986, 1997, 2000, Rosso et al. 2019, 2020a). Brachiopods occurring in dark caves include *Argyrotheca cistellula*, *A. cuneata*, *Joania cordata*, *Novocrania anomala* and *Tethyrinchia mediterranea* (Logan et al. 2004, Bitner & Gerovasileiou 2021). *Novocrania anomala*, in particular, is often found in high numbers, cemented on cave walls and ceilings (Figure 11B) (Radolović et al. 2015).

Several motile species often find shelter in dark caves, such as the mysids *Hemimysis margalefi* and *H. speluncola*, the decapods *Scyllarides latus* (Figure 11E), *Stenopus spinosus* (Figures 5F and

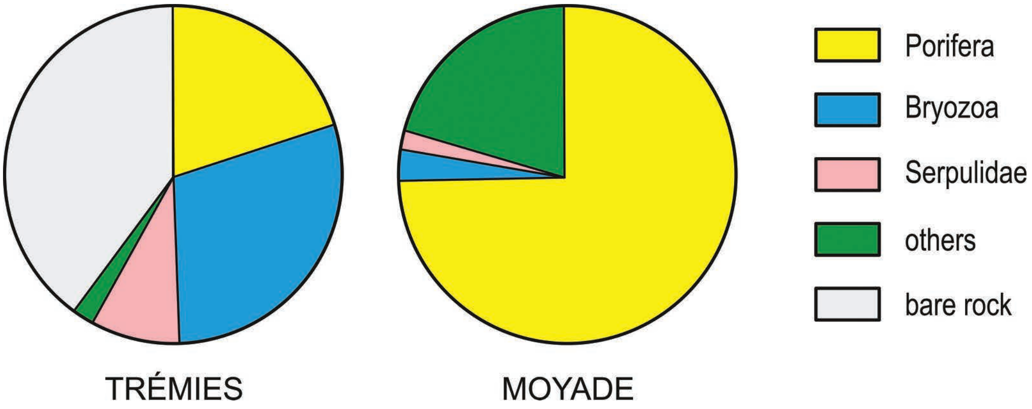

Figure 10 Per cent biological cover in two submerged marine caves of the Marseille region, France. Trémies is a blind-ended cave, and Moyade is a tunnel-shaped cave. Redrawn and modified from Harmelin et al. (1985).

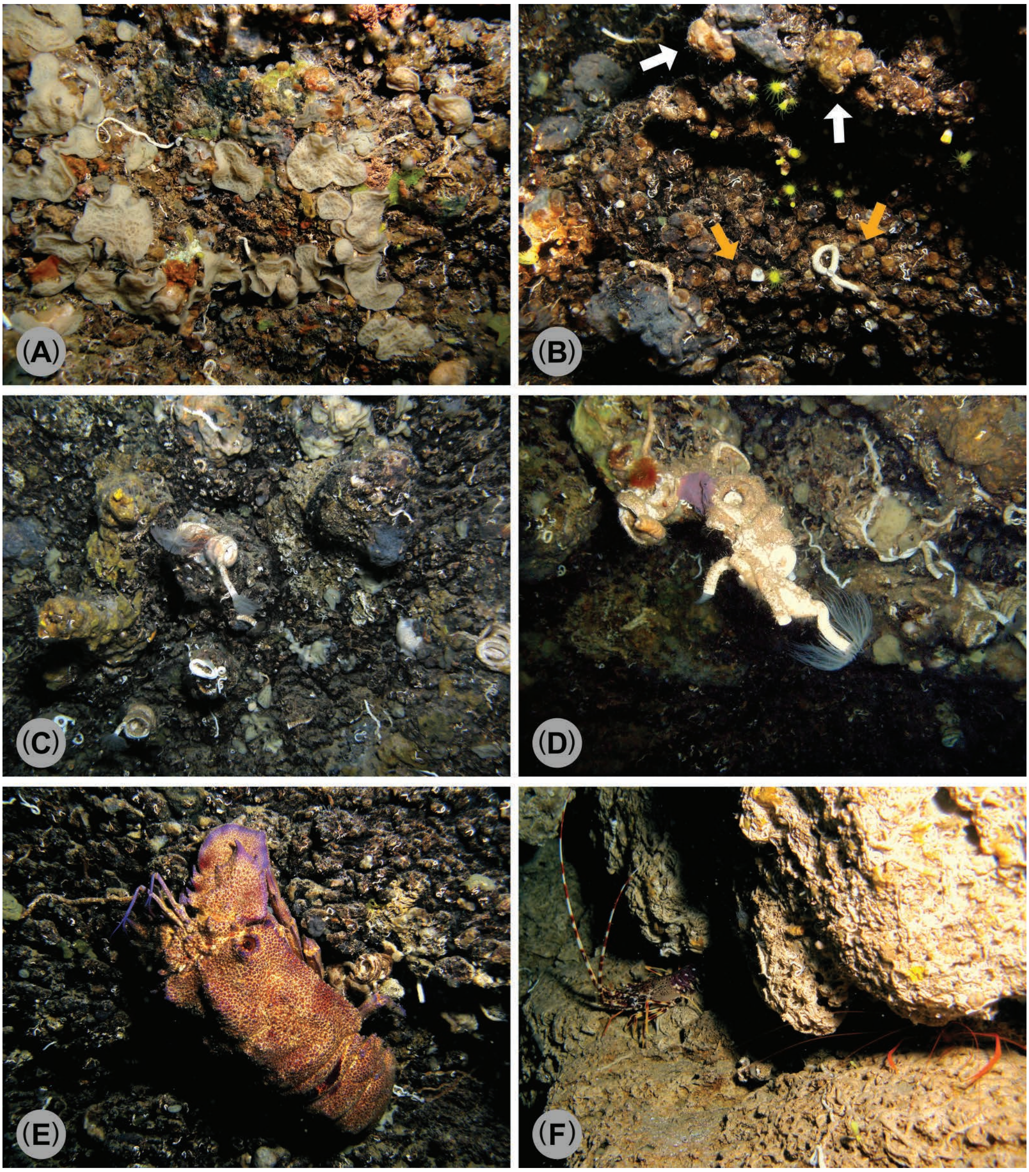

Figure 11 Aspects and species of the dark cave biocoenosis: (A) assemblage of the encrusting sponges *Plakina bowerbanki* (whitish-brownish), *Dendroxea lenis* (greyish-blue), *Hexadella* spp. (bright yellow and pale pink) and *Timea unistellata* (dull orange); (B) bryozoan nodules (white arrows), *Novocrania turbinata* brachiopod aggregations (orange arrows), *Dendroxea lenis* sponges (greyish-blue) and scleractinians *Leptopsammia pruvoti* (yellow); (C) coiled doughnut-like tube formations of the serpulid worm *Protula tubularia* and encrusting sponges (*Dendroxea lenis* and *Plakina* spp.); (D) biostalactite formed by the serpulid *Protula tubularia* and skeletons of other taxa; (E) the slipper lobster *Scyllarides latus*; (F) the decapods *Palinurus elephas* (left) and *Stenopus spinosus* (right) in a crevice of a cave wall. Photos by V. Gerovasileiou.

11F), *Palinurus elephas* (Figure 11F), *Plesionika narval* (Figure 5H; more frequent in southern and eastern Mediterranean regions), *Galathea strigosa* and *Herbstia condyliata* (Figure 5G), and the fishes *Apogon imberbis* and *Grammonus ater* (Figure 5N) (Pérès 1967, Ros et al. 1985, Bussotti et al. 2015, Gerovasileiou et al. 2015b).

The confinement zones of Bianchi & Morri

Similarly to Riedl (1966), Bianchi & Morri (1994) and Morri (2003) distinguished six ecological zones, but rather than species replacement they considered change in growth forms, trophic guilds, three-dimensional structure and biotic cover (Figure 12).

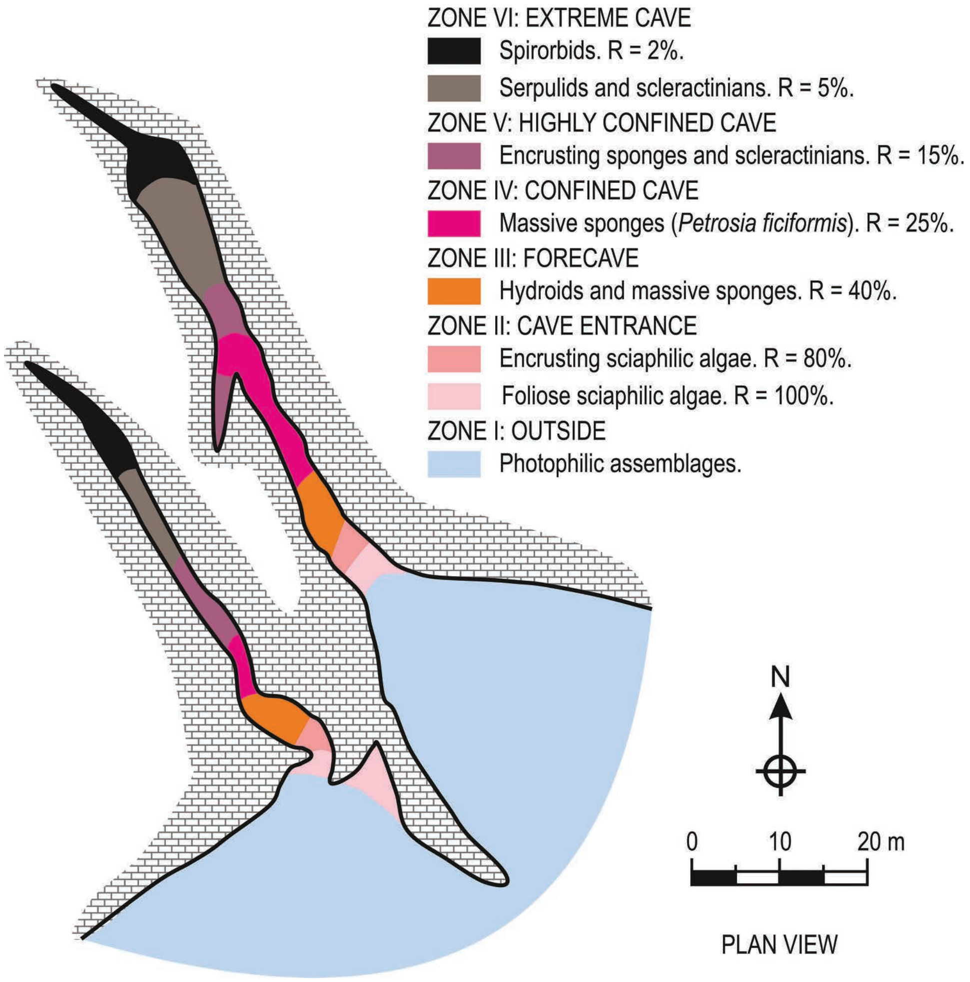

Figure 12 Zonation of the biotic assemblages of the twin caves named ‘Grotte del Bue Marino’, in the Gorgona Island (Tyrrhenian Sea, Italy) according to the confinement gradient. Cave depth is 6.5 m at the entrance and reaches 0 m in the terminal tract. R = percent cover. Redrawn and modified from Bianchi & Morri (1994) and Morri (2003).

Zone I corresponds to the ‘periphery’ of the marine cave ecosystem, consisting of the external assemblages developing close to the cave entrance; according to depth and substratum slope, they may be photophilic or sciaphilic.

Zone II represents the cave entrance and still resembles the previous zone, sharing several structural elements.

Zone III is the forecave, located shortly after the cave entrance, where macroalgae disappear and the benthic communities acquire the typical cave appearance, dominated by sessile epifauna.

Zone IV corresponds to the confined part of the cave, lacking passive suspension-feeders and dominated by submassive sponges.

Zone V encompasses highly confined sections of the cave: biotic cover is distinctly lower than 100%, and the community is composed by a thin layer of mostly encrusting organisms (sponges, bryozoans, serpulids and scleractinians).

Zone VI is an extreme environment with scattered serpulids, scleractinians and sponges; the biotic cover is lower than 10%.

A major interest of the zonation model of Bianchi & Morri is the fact that it is relatively independent of the taxonomic resolution, and can be therefore equally applied to caves of the Mediterranean or other seas: for instance, it has been tested successfully in coral reef caves of the Maldives by Bianchi & Morri (1994).

Soft substratum communities

Cave sediments are predominantly 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. scleractinians, serpulids, molluscs, bryozoans and brachiopods) present on the cave walls and ceiling (Monteiro-Marques 1981, Bianchi & Morri 2003, Rosso et al. 2013b, Pino de la Torre et al. 2020) or even from external shallow-water habitats (Di Geronimo et al. 1993). In the Grotta Marina of Bergeggi (Italy), for example, the sediments consist essentially of gravel near the outside and in the tunnel-shaped sections, and of fine sand and mud in more internal and terminal sections (Bianchi et al. 1986) (Figure 13). Thus, cave floors can represent an enclave of soft bottom within the rocky coastal system.

However, soft substratum communities of Mediterranean marine cave floors have not been studied as intensively as hard substratum ones, and there is very little information on their composition and 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 pieces of information

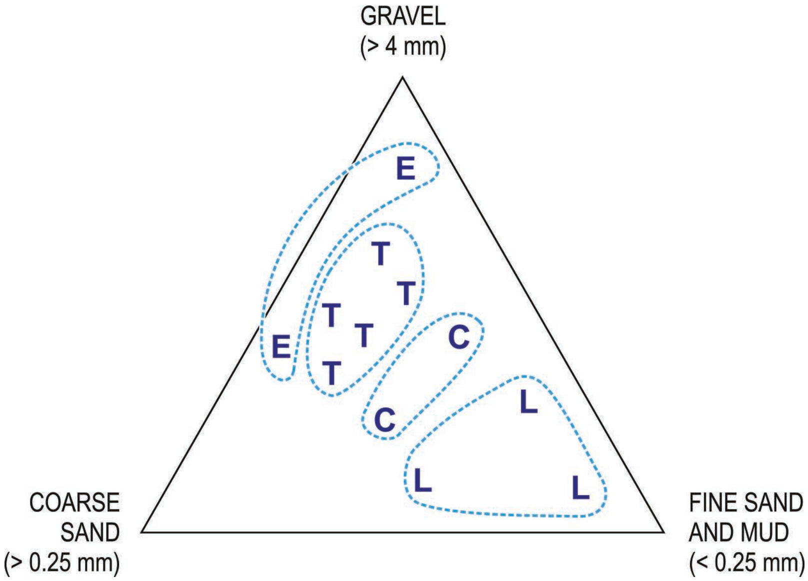

Figure 13 Ternary diagram of sediment grain size in different zones of the Grotta Marina of Bergeggi, Italy. Sediments were sampled with a diver-held corer. E=entrances; T=tunnel-shaped parts; C=lateral chambers; L=inner 'lakes'. Redrawn and modified from Bianchi et al. (1986).

on soft substratum biodiversity (including single species records, e.g. *Cerianthus membranaceus*) (Gerovasileiou & Voultsiadou 2014). According to the latter overview and updated knowledge, a total of 438 taxa have been recorded in cave sediments, mainly foraminiferans (101 species, only living material considered), bryozoans (79 taxa on detached fragments, 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 gastrotrichs (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, Pino de la Torre et al. 2020). The above studies evidenced idiosyncratic patterns in each cave, so that the structure of soft-bottom communities inside marine caves is difficult to generalize.

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). 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 bilineata*. 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, the Grotta Azzurra of Cape Palinuro (Italy). Its peculiarity derives both from the presence of sulphur hydrothermal springs, mainly located in the inner dark chamber 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). 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 sections, indicating differences at a scale of a few metres. However, there was no clear inward decline of abundance, biomass or diversity, suggesting that the chemosynthetic inputs in the inner cave chamber provide an additional trophic supply, thus having a positive effect on benthic assemblages. The abundance of taxa which are considered as indicators of environmental instability (e.g. the polychaetes *Paradoneis lyra*, *Levinsenia gracilis* and several species of the family Capitellidae, and the bivalves *Corbula gibba* and *Thyasira flexuosa*) indicated the excess of organic matter enrichment, similarly to the sediments in marine caves of Marseille region (Monteiro-Marques 1981).

In addition to the infauna, an abundant epifauna (fixed or sedentary) was found in the Grotta Azzurra floor, such as the bivalve mollusc *Pinna nobilis*, the tubiculous polychaetes *Phyllochaetopterus socialis* and *Sabella pavonina*, the echinoderms *Antedon mediterranea*, *Stylocidaris affinis* and *Ophioderma longicaudum* (Figure 14A) (Bianchi & Morri 2003). Bianchi et al. (1994) suggested that this unusual abundance of suspension-feeding and detritivorous epifauna was related to the chemosynthetic production by the sulphur bacteria in this particular environment.

Certain large tube-dwelling or burrowing anthozoans can be also common on the sedimentary bottoms of marine caves (Morri et al. 1991). *Cerianthus membranaceus* is known from several Mediterranean caves (Figure 14B). *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 Grotta della Cala di Mitigliano, in the Tyrrhenian Sea (Boero et al. 1991).

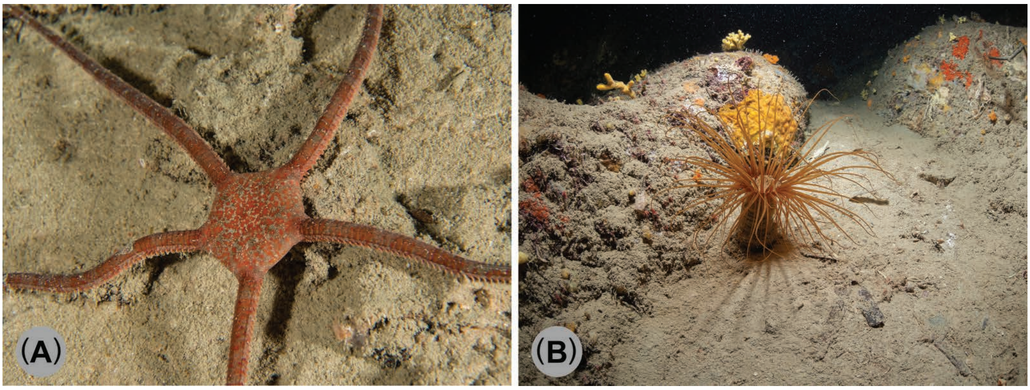

Figure 14 Typical epifaunal invertebrates on soft cave sediments: (A) the detritivorous brittle star *Ophioderma longicaudum*; (B) the tube-dwelling anemone *Cerianthus membranaceus*. Photos by T. Dailianis.

There have been recent studies of the soft substratum macrofauna of Mediterranean marine caves along 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 cave interior and adjacent external sites. None of the species exhibited a significant preference for caves, although amphipods of the genus *Harpinia* dominated inside the marine caves. In all caves, external sediments, which were coarser, had higher species richness. Diversity was significantly lower inside caves, where the percentage of silt and clay was significantly higher. However, this was not the case for abundance, which was low only in deeper caves, while in the shallower ones, the total 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 external sites to a greater degree. 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).

Meiobenthos

Meiobenthos has been rarely studied in Mediterranean marine caves. Specifically, only a few studies have investigated spatial variability of meiobenthos, on soft (e.g. Todaro et al. 2006, Janssen et al. 2013, Ape et al. 2016, Romano et al. 2018, 2020) and hard substrata (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).

Todaro et al. (2006) studied meiofauna in three dark sites of the Grotta di Ciolo (Salento, Italy), at horizontal distances of 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 per 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, and particularly of harpacticoid copepods, decreased inwards, thus indicating that meiobenthic community is structured in accordance with the trophic depletion hypothesis.

Janssen et al. (2013) studied the meiofauna of the sediments of the 3PP Cave (Marseille region, 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 undescribed. There were significant quantitative and qualitative differences in the composition of copepod assemblages between the three stations, at the family, genus and species levels. 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 (Figure 15).

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 the exclusive species *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.

Studies on benthic foraminiferans in two marine caves of Orosei Gulf (Sardinia), Bel Torrente (BT) and Bue Marino (BM), showed that benthic foraminiferans may live in cave environments, even at a considerable distance from the entrance, while their distribution and community structure is affected by environmental gradients (Bergamin et al. 2018, Romano et al. 2018, 2020). In the BT cave, benthic foraminiferans were found as far as 330 m from the cave entrance, while the inner sections were totally barren (Romano et al. 2018). A total of 106 species were recorded (76 species had living individuals), with the most abundant being *Gavelinopsis praegeri*, *Nodulina dentaliniformis*, *Eggerelloides advenus* and *Ammonia inflata*. In the BM cave, benthic foraminiferans were found along the first 450 m of the cave (Romano et al. 2020). In total, 108 species were found (52 species had

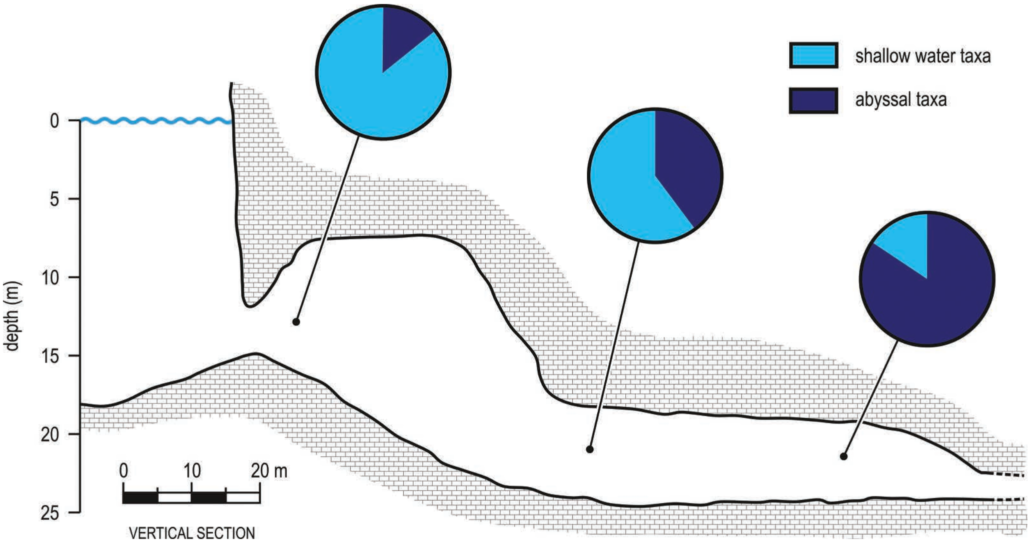

Figure 15 Proportion of copepod species with affinity for shallow or abyssal waters in different zones of the 3PP Cave of Marseille region, France. Redrawn and modified from Janssen et al. (2013).

living individuals), with the most abundant being *Nouria polymorphinoides*, *Eggerelloides advenus*, *Rosalina bradyi* and *Gavelinopsis praegeri*. None of the recorded species are cave-exclusive, and the colonization of caves probably took place through transport from the open sea of juvenile specimens in a cryptic stage (Bergamin et al. 2018). Common taxa from external coastal areas were found only close to the entrance, while inside the caves foraminiferans were exclusively epifaunal clinging/attached or opportunist infaunal species, which tolerate a wide range of environmental parameters, possibly generated by episodic freshwater inflow (Romano et al. 2018). In both caves, density and species diversity decreased inwards and were associated with gradients of physicochemical parameters. More specifically, salinity was found to affect the assemblage structure, and water acidification was suggested to cause a shift from a calcareous hyaline-dominated assemblage to an agglutinant-dominated one (Romano et al. 2018). In the BM cave, three 'ecozones' were identified (i.e. entrance, confluence and a transitional ecozone), while foraminiferans were absent from the inner cave zones (Romano et al. 2020). All the ecozones were characterized by the presence of hyaline, porcelaneous and agglutinated taxa, which however had different relative abundances in each ecozone. In the entrance ecozone, hyaline taxa dominated, while agglutinated taxa were more abundant in the two other ecozones. Porcelaneous taxa covered only a minor percentage of the total assemblage in all ecozones. A single species, *Nouria polymorphinoides*, was extremely abundant in the confluence ecozone, perhaps exhibiting opportunism in response to the high input of plant debris after a period of high rainfall (Romano et al. 2020).

Environmental and 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 metres. Gradients are recognizable in both physicochemical factors and biological aspects.

Main environmental gradients

Light availability

The decrease of light obviously plays a pivotal role in shaping community structure and species distribution in marine caves, constituting a limiting factor for the development of macroalgae 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. 2017b). Light level has been traditionally used for distinguishing the two marine cave biocoenoses, those of semidark 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 the limit for algal development is around 0.5–1% of the surface illumination (Riedl 1966) while, according to Harmelin et al. (1985) and Bianchi et al. (1986), animal-dominated communities develop in cave sections where light intensity is <1% of the sunlight at the sea surface and the dark cave biocoenosis develops where light levels are lower than 0.01% of the sea-surface levels, respectively. Observations and measurements made by Southward et al. (1996) at the entrance of the Grotta Azzurra of Cape Palinuro showed that with light equal to 17% of that of surface, the assemblages are still dominated by photophilic algae, in particular by Phaeophyceae (*Dictyota*). At 3%, the assemblage becomes sciaphilic, dominated by Rhodophyta (*Peyssonnelia* and encrusting coralline algae), while below 0.8%, the assemblage consists exclusively of sessile animals, with sponges, hydroids, scleractinians, bryozoans and colonial ascidians (Figure 16). Of course, the decrease in ambient light depends not only on the distance from the entrance, but also on the topographic position (e.g. floor, walls or ceiling).

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

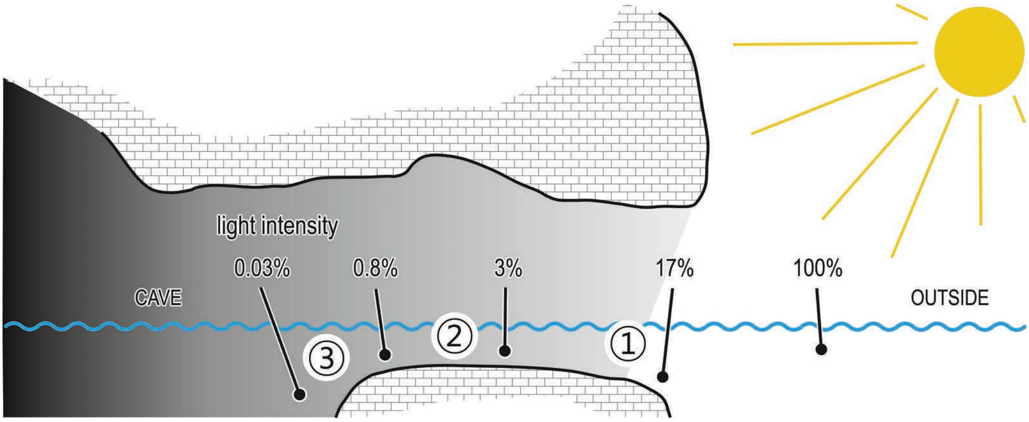

Figure 16 Reduction in light intensity and biological zonation at the entrance of the Grotta Azzurra of Cape Palinuro, Italy. Light intensity is expressed as a percentage of the surface value. (1) Community of photophilic algae; (2) sciaphilic algal assemblage (encrusting rhodophytes); (3) exclusively animal assemblage. Redrawn and modified from Southward et al. (1996) and Morri & Bianchi (2003).

with depth (e.g. shallow versus deep caves) and is affected by cave-specific topographic features. According to Riedl (1966), the exposure to light of a marine cave is affected by five factors: surface illumination, depth, orientation with respect to the cardinal points (i.e. aspect), vertical angle of the plane of the entrance and slope of the main axis of the cave. The entrance width to cave length ratio, and the position and number of entrances and secondary openings can also affect light intensity in caves. Thus, entrance zones in shallow semi-submerged caves and tunnels with multiple openings receive more sunlight compared with 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. 2017b).

Water circulation and associated parameters

The study of tunnel-shaped caves shows 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 substratum in dark zones (Riedl 1966, Harmelin 1969, Harmelin et al. 1985). Therefore, it has been argued 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 sections. Based on current measurements and accurate topographic data, which allowed the cave geometry to be reconstructed, Bianchi et al. (1998) calculated the water balance of the Grotta Azzurra (Tyrrhenian Sea, Italy). In the tunnel-shaped section 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, water was exchanged only by diffusion. A particle of water that travels along the entire perimeter of the chamber would take more than 2.5 hours under calm seas but only 15 minutes in the presence of a current speed of 10 $\text{cm}\cdot\text{s}^{-1}$. 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 depends not 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 formation 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 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 1 hour and a cave of 1 m^3 for only 8 minutes (Riedl 1966). Thus, due to the limited amount of autochthonous primary production, cave communities greatly depend on external food supply. Since benthic communities in caves are dominated by suspension-feeders, this food will essentially be represented by the organic substance suspended in the water. These considerations lead to the trophic depletion hypothesis, which states that cave fauna in more confined environments with limited water circulation will have a significantly lower food intake (Zabala et al. 1989, Bianchi et al. 2003).

Current speed

Long-term measurements of water movement in Mediterranean Sea caves are lacking, although there have been a few short-term studies (normally over periods of less than 24 hours). These few examples measured unidirectional flows, especially in tunnel-shaped caves, but different wave regimes are likely to cause significant variability in water movement patterns inside caves with complex morphologies. Pansini & Pronzato (1982) and Balduzzi et al. (1989) estimated water movement in the blind-ended Grotta della Cala di Mitigliano (Tyrrhenian Sea, Italy), using plaster balls, whose dissolution rate 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 equivalent velocity in $cm \cdot s^{-1}$, M is the % weight loss of the balls after 24 hours, and B is the % weight loss of the reference balls, placed in still water), Sgorbini et al. (1988) calculated the equivalent current speed in the Grotta Marina of Bergeggi (Ligurian Sea, Italy). Due to the general tunnel-like shape of this cave, the flow (as indicated by release of dye from the plaster balls) was unidirectional from sections with the shallowest water depth to the deepest. Current speed varied little throughout the cave (12–20 $cm \cdot s^{-1}$), except in internal 'lakes' and lateral chambers where water flow was significantly slower (Figure 17). In the same cave, Morri et al. (1994a) found a significant positive correlation between the values of equivalent 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 meters and found that during calm sea conditions, the current was directed towards south-east with a velocity of <2 $cm \cdot s^{-1}$. During slightly rough sea conditions, with winds blowing from the north-east quadrant, current inside the cave was directed towards south-west with a velocity of 6–10 $cm \cdot s^{-1}$. Faster currents are expected with greater wave height.

According to Riedl (1966), the intensity of water movement at a specific point in a cave depends on four factors: coast exposure and profile, depth, form and nature of the substratum. Riedl (1966) suggested that the development of typical cave communities requires a water agitation of no more than 2–10% of that of the surface. The shape of the cavity can accelerate (narrows) or slow down (widenings) the motion of water, which is reflected in the distribution of indicator taxa (e.g. hydroids) or the occurrence of erosional features in the rock. Several studies have suggested that the reduced sponge morphological diversity (i.e. dominance of encrusting growth forms) and species diversity

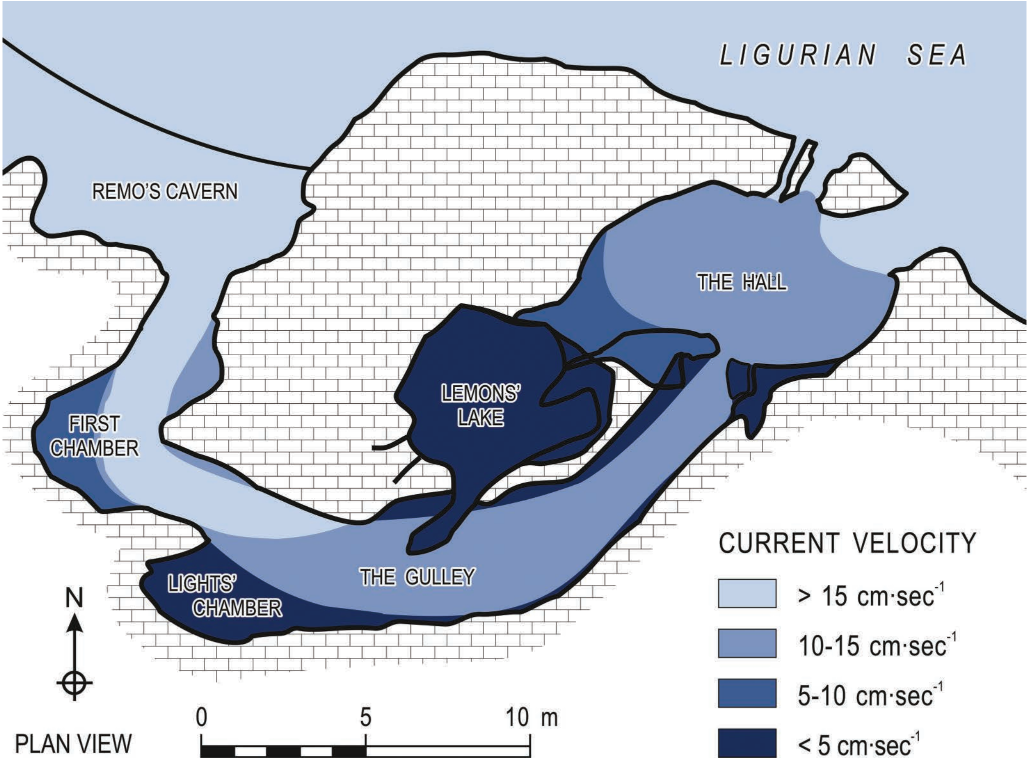

Figure 17 Current equivalent velocity in different zones of the eastern branch of the Grotta Marina of Bergeggi, Italy. In the tunnel-shaped part of the cave, the flow is mostly directed towards south-east. Redrawn and modified from Bianchi et al. (1986) and Montefalcone et al. (2018).

in the intermediate corridors of marine caves are related to the locally stronger flow rates due to the Venturi effect (i.e. the velocity of a fluid increases as the cross-sectional area decreases), which is caused by the cave narrowing (Pansini et al. 1977, Bell 2002, Gerovasileiou & Voultsiadou 2016).

Water temperature

Water temperature inside marine caves depends on several parameters, such as geographical location, local environmental conditions, water circulation, exposure to the open sea, cave morphology and bathymetry, presence of internal springs and freshwater infiltrations. Water temperature difference between the inner sections of marine caves of Marseille region (France) and the external environment could reach up to 7 °C, with temperature fluctuations being greater in the entrance zone (Pouliquen 1972, Harmelin et al. 1985, Passelaigue & Bourdillon 1985). Bianchi et al. (1986) took monthly temperature measurements in the Grotta Marina of Bergeggi (Italy): the innermost portions of the cave exhibited less variable temperatures (14–20 °C) all year-round with respect to the entrance zone (12.5–22.5 °C) (Figure 18). 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 water stratification despite the fact that the cave is shallow and exposed to the open sea. More specifically, they observed the retention of different water bodies in different parts

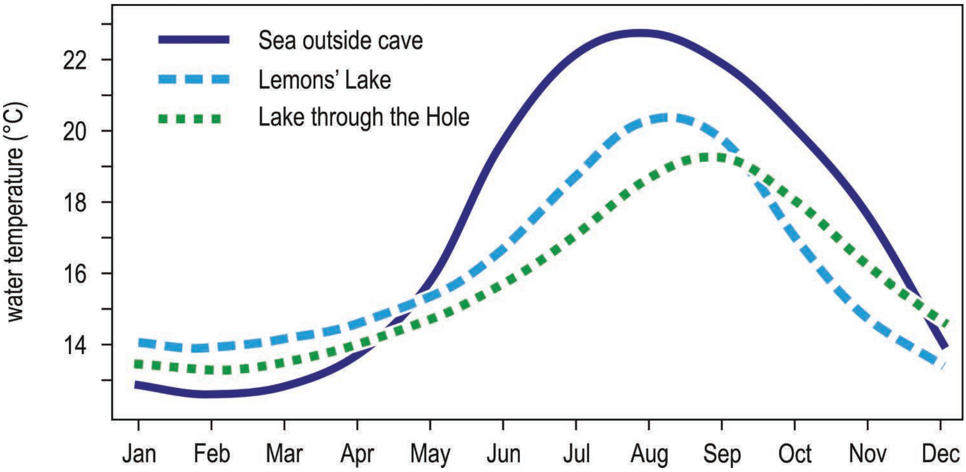

Figure 18 Annual trends of monthly water temperatures in the sea outside and in the highly confined inner 'lakes' of the Grotta Marina of Bergeggi, Italy. Redrawn and modified from Bianchi et al. (1986).

of the cave: a colder water layer on the bottom of the cave interior during summer, attributed to the cave morphology; brackish water (18–22 PSU) on the sea surface in an intermediate semi-submerged chamber during summer; and warmer water (>15 °C) in upper parts of the cave during winter, possibly due to the mixing of freshwater and seawater. Romano et al. (2020) studied two marine caves in Sardinia, Bel Torrente and Bue Marino and found that their mean water temperature was 24.9±0.5 °C and 24.2±0.2 °C, respectively, in the summer of 2014, whereas it was 19.7±0.4 °C and 17.0±0.3 °C, respectively, in the spring of 2015.

The 3PP Cave near Marseille, France, provides a good illustration of the role of cave morphology in thermal stratification of water inside caves. The cave slopes downwards from the entrance, 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 thermohaline stratification: the inner cave chamber is filled with cold, density-trapped seawater which remains at a nearly constant temperature all year (12.8–14.5 °C) compared with 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).

The maximum water temperatures recorded from caves of the Marseille region, which slope upwards from the entrance, reach up to 24 °C, usually for relatively short periods (Chevaldonné & Lejeusne 2003). 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 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 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 that receive freshwater input, temperature in the seawater layer reached 27–28 °C while in the freshwater layer, it was 21 °C (September 2002 and July 2003, data in Pérez et al. 2004). In a marine cave in the Levantine coasts of Turkey (Antakya Bay), water temperature was 28 °C at the entrance of the cave and 21–22 °C in the terminal chamber, where an internal freshwater spring is present, while in winter, temperature at the entrance is about 16 °C and 21 °C in the terminal chamber (Turan et al. 2019).

Freshwater input

In some caves, freshwater infiltrations (usually sporadic or seasonal) in the inner and upper portions (e.g. cave ceilings of 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 PSU (in March and September, respectively) while its values at the entrance and outer chamber were 38.1–38.4 PSU. In the most confined parts of the Grotta Marina of Bergeggi (Italy), the infiltration of rainwater through the karstic network creates inner 'lakes' where the salinity can fall to 13.6–17.6 PSU during calm seas, to acquire a near normal marine salinity of 34.9–37.5 PSU during periods of greater wave action, which causes complete water renewal in the whole cave (Bianchi et al. 1986).

The occurrence of some rare sessile taxa and bioconstructions only in a small number of caves with freshwater input is possibly related to either salinity gradients or the provision of organic material and nutrients. Such cases include the rare scleractinian *Guynia annulata* in marine caves of Marseille region and Crete (Zibrowius 1978), the development of 'biostalactites' by the serpulid *Protula tubularia* in caves of Italy, Greece and Cyprus (Belmonte et al. 2009, 2020, Guido et al. 2014, 2017a, 2019a,b, Sanfilippo et al. 2015, 2017, Ingrosso et al. 2018, Jimenez et al. 2019, Rosso et al. 2021, V. Gerovasileiou, unpublished data), and lithistid sponges in shallow marine caves of Greece (Pisera & Gerovasileiou 2018, 2021 and unpublished data by V. Gerovasileiou). This association between dense populations of lithistids, originating from adjacent deep-water populations whose propagules were upwelled to shallow caves with freshwater influx, is probably explained by the rich silicate content in water (up to 11 times higher than outside caves and comparable to deep seawater at several hundred metres depth), delivered to the caves by freshwater sources, that promotes the development of these hypersilicified sponges (Pisera & Gerovasileiou 2021).

Seasonal freshwater floods were also found to affect the distribution and assemblage structure or benthic foraminiferans in marine caves of Sardinia (Bergamin et al. 2018, Romano et al. 2018, 2020).

Sedimentation

Cave walls in highly confined chambers with a little water movement, 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 (Figure 8C). These surfaces are usually colonized only by a small number of sessile taxa which can tolerate high levels of sedimentation (Laborel & Vacelet 1958, Pouliquen 1972, Zabala & Gili 1985, Gerovasileiou & Voultsiadou 2016, Gerovasileiou et al. 2017b, 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). High rates of sedimentation were the main factor affecting polychaete distribution in a marine cave of the Sorrentine Peninsula, Tyrrhenian Sea, Italy (Belloni & Bianchi 1982).

Biological gradients

In 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 caves (Harmelin et al. 1985, Balduzzi et al. 1989, Martí et al. 2004a, Gerovasileiou & Voultsiadou 2016, Gerovasileiou et al. 2017b).

Biological cover and abundance

One of the most widely used parameters for the quantification of benthic community patterns on hard substrata is the biotic cover, i.e. the percentage of substratum occupied by living organisms, as a measure of organismal abundance. From values around 100%, typical of the external environment, biotic cover progressively decreases and can even approach zero in the terminal sections 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. 2017b). Based on biotic cover, Laborel & Vacelet (1959) 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 semidark to the dark cave section, and to the reduction of water movement within the inner dark section (Figure 19A–B). On the other hand, in tunnel-shaped caves with constant water renewal, biotic cover could reach 100% of the hard substrata even in the totally dark zone (Figure 19C) (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. 2017b, Dimarchopoulou et al. 2018).

The only existing study on hard substratum meiofauna has shown that while abundance decreased from the entrance to the middle part of the 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: thus, spatial patterns of abundance cannot be generalized.

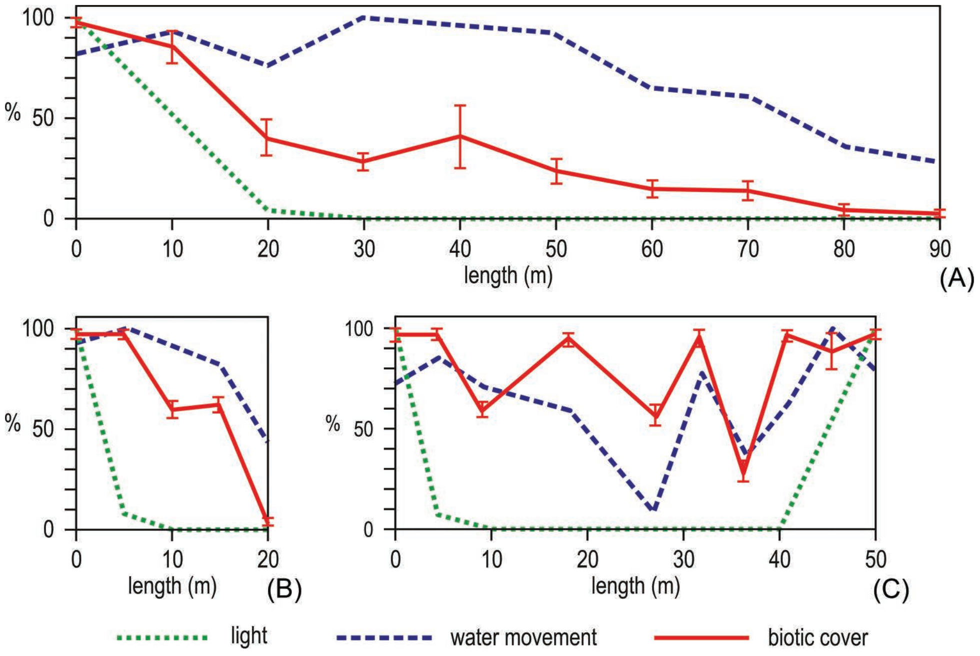

Figure 19 Differences between blind-ended caves (A, B), independently of their length, and tunnel-shaped caves (C), considering light penetration, water movement intensity and biotic cover (mean±standard error), from the entrance to the innermost portions of the caves. Light and water movement are expressed as percentage of the maximum value measured. (A) Grotta della Cala di Mitigliano (Tyrrhenian Sea); (B) and (C) Grotta Marina of Bergeggi (Ligurian Sea). Redrawn and modified from Morri & Bianchi (2003), based on original data by Balduzzi et al. (1989) and Morri et al. (1994a).

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 the 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 (Tyrrhenian Sea, Italy), a blind-ended cave over 80 m long, with sessile species number shifting from 60 to 10 (Figure 20). However, in several studies, diversity increased from the well-lit entrance to the semidark sections and then decreased inwards (Sarà 1962, Cinelli et al. 1977, Corriero et al. 1997b, 2000, Bell 2002, Gerovasileiou & Voultsiadou 2016, Dimarchopoulou et al. 2018), or even kept increasing to the innermost cave sections (Martí et al. 2004a,b), which were characterized by rich animal-dominated communities. Such divergent patterns were generally attributed to cave-specific topographic features which generate gradients of abiotic and biotic features.

Of course, these trends vary with the taxon under consideration, different groups dominating in different cave sections.

Regarding macroinfauna and meiofauna, the few existing studies have shown contrasting results, and thus, spatial patterns of diversity cannot be generalized. Macroinvertebrate assemblages

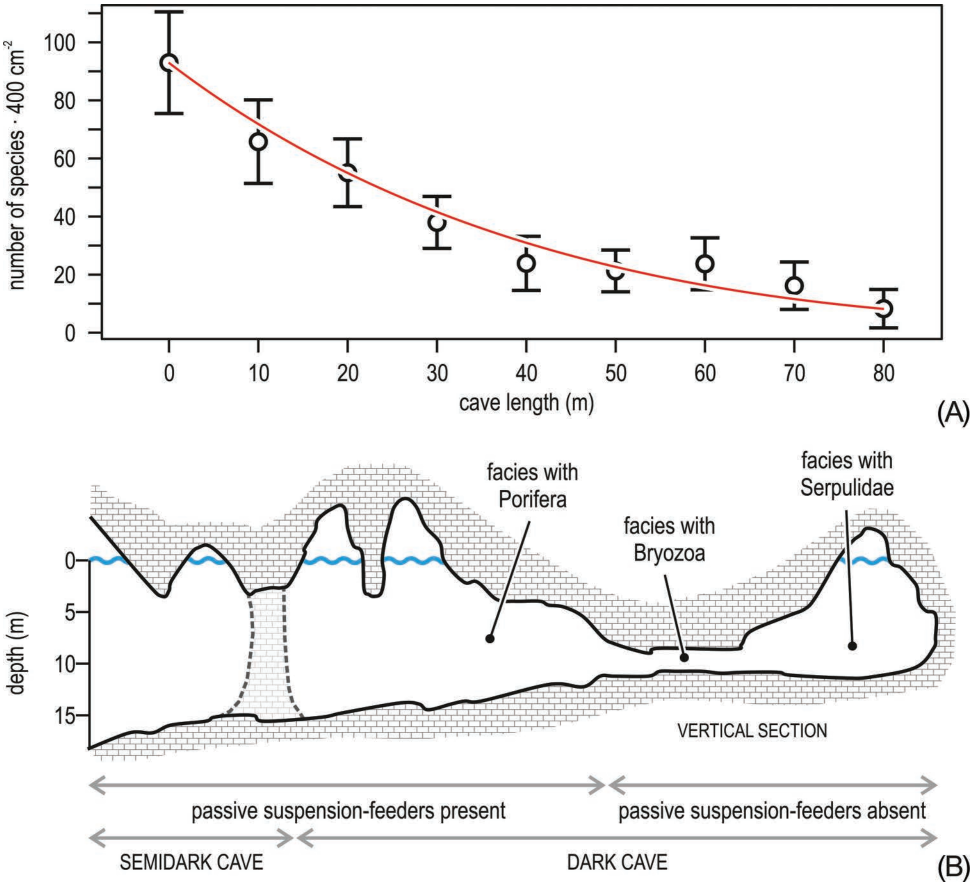

Figure 20 Decrease in species richness (A) and ecological zonation (B) in the blind-ended cave of the Cala di Mitigliano, Italy. Redrawn and modified from Balduzzi et al. (1989), Bianchi et al. (1996) and Morri & Bianchi (2003).

associated with sponges in marine caves in Lesvos Island, Aegean Sea (Gerovasileiou et al. 2016c) and hydrozoans in the Alboran Sea (Navarro-Barranco et al. 2014) were found to exhibit an inwards decrease in species richness.

Biomass

Although biomass (i.e. the quantity by weight of living matter per unit area) has rarely been measured in marine caves, a sharp decrease from the entrance towards the cave interior has been evidenced, as for biotic cover and diversity (True 1970, Gili et al. 1986, Fichez 1989, 1990b, Zabala et al. 1989). Gili et al. (1986) studied a blind-ended cave in the Medes Islands (Catalonia, Spain) and found that biomass, expressed as ash-free dry weight per square metre, decreased from the entrance (0.26 kg·m^{-2}) to the inner portion (0.08 kg·m^{-2}). Measurements carried out in the Grotte des Trémies (Marseille region, France) by Fichez (1989) showed that from the semidark to the dark cave zones, there was a >90% reduction in biomass. Specifically, the infaunal biomass declined from 3.4 ± 0.4 g·m^{-2} to 0.3 ± 0.2 g·m^{-2}, while the epifaunal biomass declined from 305.1 ± 33.6 g·m^{-2} to 29.7 ± 22.0 g·m^{-2}.

Volumetric stratification

Increasing confinement and subsequent oligotrophy towards the innermost dark cave sections 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. 2017b). 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 taller than 1 dm (Figure 21), with gorgonian species (e.g. *Eunicella cavolini* and *Paramuricea clavata*) protruding into the water column for >0.5 m (Harmelin et al. 1985, Morri & Bianchi 2003). In the semidark cave sections, the height of the upper layer reduces to a maximum of 10–20 cm in the case of well-developed populations of red coral (*Corallium rubrum*). In the inner cave sections, the benthic community may appear monolayered, even in the case of 100% substratum cover, but in the transitional zone to the dark zone, it can 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 part arises from the substratum into 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. 2016c, 2017b).

A biological scale of hydrological confinement

As pointed out by Guelorget & Perthuisot (1983, 1992), hydrological confinement is a complex and rather abstract quantity, which cannot be accurately expressed with numbers. Confinement is mainly a hydrodynamic notion, essentially related to water exchange, but measurements of current speed and estimates of water budget in different Italian caves demonstrated that it definitely depends on both shape and size of the cavity (Morri 2003). Similarly to what had been already done for coastal lagoons by Guelorget & Perthuisot (1983, 1992), Bianchi & Morri (1994) defined a biologically based confinement scale for marine caves, taking into consideration three easily quantifiable biological parameters: (1) the structural and functional composition, as expressed by the dominant growth forms and trophic guilds, respectively; (2) the spatial organization, and above all the presence of an upper layer in the vertical development of the species assemblage; and (3) the total biotic cover of the substratum. Bianchi & Morri (1994) carried out a first test of the biological confinement scale in the Grotte del Bue Marino in the Island of Gorgona (Leghorn, Italy), two parallel caves with a predominantly subhorizontal development. The morphological characteristics of these caves, and

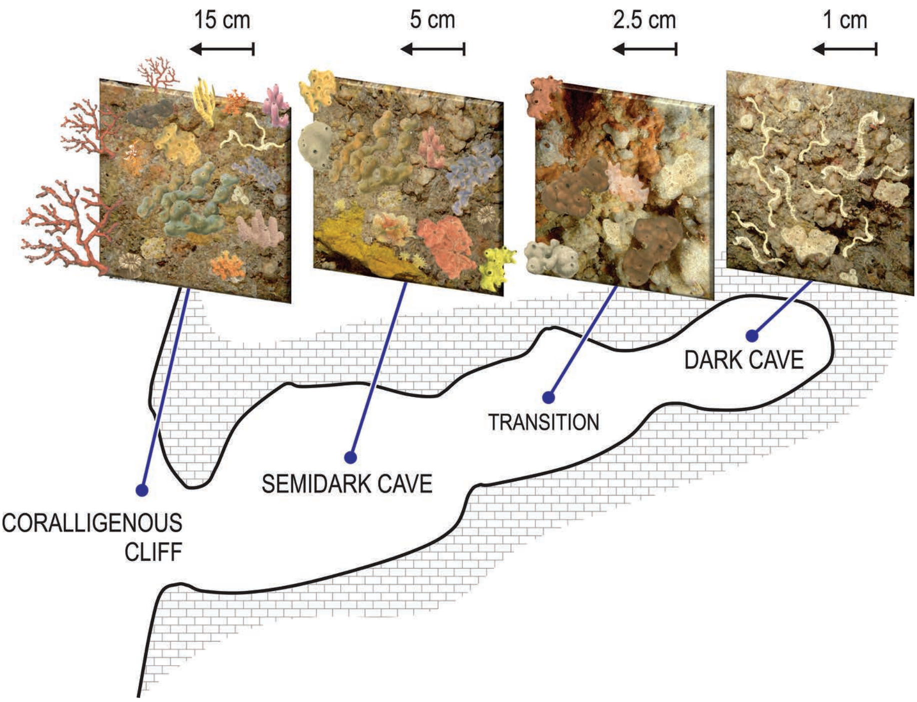

Figure 21 Loss of three-dimensional complexity in the biotic cover of blind-ended marine caves. Erect growth forms higher than 15 cm characterize the coralligenous biocoenosis at the cave entrance and are replaced by massive organisms typically not exceeding 5 cm height in semidark caves; in the transitional zone, when present, bryozoan nodules and submassive sponges may reach 2.5 cm height, whereas the dark cave biocoenosis is inhabited by encrusting organisms that may only arise 1 cm from the substratum (e.g. the terminal parts of serpulid tubes). Redrawn and modified from Harmelin et al. (1985). Animals illustrated as examples have been taken from original drawings by Toni Llobet (Ballesteros & Llobet 2015).

specifically the fact that they both have a simple linear development and blind-ended shape, can be considered as paradigmatic conditions of hydrological confinement. In addition, the fact that these are two adjacent 'twin' cavities appeared advantageous to compare directly the biological zonation observed (Figure 12):

- Degree 0 is located upstream of zone I, in the external environment.
- Degree 1 corresponds to the transition between zones I and II, at the cave entrance, and is marked by the simplification of the assemblage structure, especially by the reduction of the upper layer.
- Degree 2 is recognizable by the radical modification of the assemblage (disappearance of macroalgae), which begins to exhibit a typical cave appearance, and is situated between zones II and III.
- Degree 3 lies between zones III and IV and is indicated by the disappearance or extremely low abundance of passive suspension-feeders, especially the erect ones.
- Degree 4, between zones IV and V, corresponds to the disappearance or severe decrease of massive forms.
- Degree 5 witnesses the disappearance of sheet-like encrusting forms, between zones V and VI.
- Degree 6 is reached when all sessile fauna disappears.

Anchialine caves are characterized by highly confined conditions, beyond degree 6 of the scale above.

Ecosystem functioning

Trophic depletion

With the exception of the few caves that host chemosynthetic bacteria and the entrance sections where algae may be present, semidark and dark cave assemblages are sustained by secondary production only, due to the lack of light and the consequent absence of photo-autotrophic organisms (Riedl 1966). Even if algal filaments reach the inner semidark and dark sections of marine caves, advected by currents or waves, they fail to survive due to the lack of light (Moscatello & Belmonte 2007). Therefore, marine cave assemblages typically depend on the input of matter and energy from the external environment. By drawing their nourishment from the water column, suspension-feeders (active and passive) are the secondary producers that assimilate organic matter and energy coming from outside the cave, where it was produced, and make it available to higher trophic levels inside (Ott & Svoboda 1978, Bibiloni et al. 1984, Balduzzi et al. 1989, Bianchi 1994, Rastorgueff et al. 2011, 2015a). This explains their qualitative and quantitative dominance, which is a typical feature of all marine caves (Ott & Svoboda 1978, Bibiloni et al. 1984, Bianchi 1985). 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. Thus, the most confined caves or cave sections 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 trophic depletion hypothesis was illustrated in the Grotta Marina of Bergeggi, Italy (Bianchi et al. 1986, Morri et al. 1994a), and in marine caves near Marseille, France (Fichez 1989, 1990a,b,c, 1991a,b,c). The extreme impoverishment of the dietary intake observed in the confined zones of the caves occurs through both the quantitative decrease of the nourishment (e.g. lower absolute quantity, reduction of the supply) and its qualitative degradation (e.g. high carbon/nitrogen ratio, greater proportion of complex compounds, decrease in the percentage of sugars, decrease in the ratio between chlorophyll *a* and phaeopigments) (Bianchi & Morri 1999).

Decrease in food quantity

The amount of total particulate matter, as well as the organic carbon and nitrogen it contains, decreases significantly from the semidark 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 suspension-feeders (Fichez 1991c, Palau et al. 1991, Garrabou & Flos 1995, Rastorgueff et al. 2011, 2015a). The abundance of the suspension-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 enough energy to support an abundant benthic fauna. The situation can change during the spring season, when the warming of the open sea generates a rapid mixing of the waters with concomitant new influx of organic matter, in particular of phytoplankton (Fichez 1989, 1990b). The importance of phytoplankton in the suspended particulate material that penetrates 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 (Ligurian Sea, Italy)

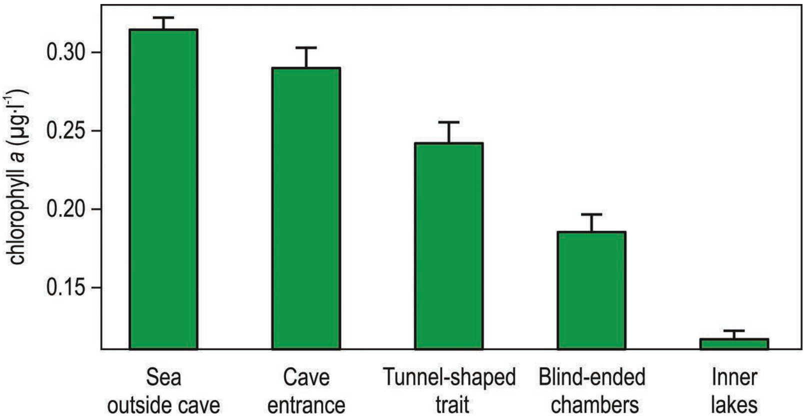

Figure 22 Chlorophyll *a* concentration in different zones of the Grotta Marina of Bergeggi, Italy. Redrawn and modified from Bianchi et al. (2003), based on data in Morri et al. (1994a).

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 (Figure 22); 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 correspond well with the hydrological confinement gradient (Bianchi & Morri 1994).

Degradation of food quality

Moving from a semidark cave to a dark cave, not only does the total amount of organic matter decrease, but its composition changes also, with a reduction in the nutritional value of organic matter (Table 3).

- The ratio between the carbon content and the nitrogen content (C/N ratio) is an index of the nutritional value of the organic matter. Food with high carbon and little nitrogen content (e.g. cellulose) is less nutritious than food that is proportionally richer in nitrogen (e.g. proteins). Both in the Grotte des Trémies (Marseille region, France) and in the Grotta Marina of Bergeggi (Liguria, Italy), the C/N ratio tends to increase inwards (Figure 23), indicating a decrease in the food value of the suspended particulate matter (Morri et al. 1994a).

Table 3 Values of some indicators of quantity and quality of the trophic input in the Grotte des Trémies, near Marseille, France

Indicator	Semidark cave	Dark cave
Total particulate (µg·L^{-1})	1711±33	1263±48
Organic carbon (µg·L^{-1})	81.8±9.0	44.4±2.7
Organic nitrogen (µg·L^{-1})	9.3±1.2	4.3±0.3
C/N ratio	8.8±0.2	10.3±0.1
Carbohydrates (mcal·L^{-1})	123±20	48±6
Proteins (mcal·L^{-1})	187±16	89±5
Lipids (mcal·L^{-1})	312±41	135±11
Simple/complex organic matter ratio	4.1±0.6	2.3±0.1
Chlorophyll/phaeophytin ratio	256.4±159.5	5.9±0.9

Source: From Bianchi et al. (2003), based on the elaboration of data taken from Fichez (1989).

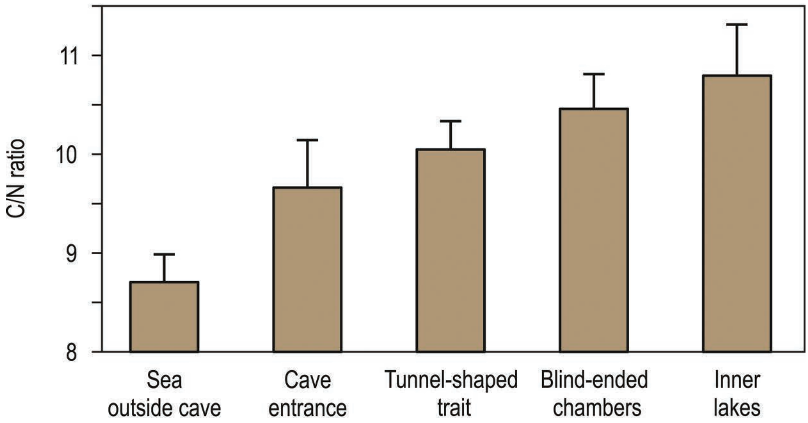

Figure 23 Food quality (expressed as carbon/nitrogen ratio), in different zones of the Grotta Marina of Bergeggi, Italy. Redrawn and modified from Bianchi et al. (2003), based on data in Morri et al. (1994a).

In both caves, the C/N ratio is lower than 17, a threshold value for animal consumption (Russel-Hunter 1970, Cocito et al. 1990). The study of the C/N ratio in the suspended particulate matter of two marine caves of Marseille region by Rastorgueff et al. (2011) showed that the ratio was higher 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 inside the entrance. The high C/N value inside the 3PP 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 external 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 sections, 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 proportions of heteropolycondensates, geopolymers, marine humic substances and other complex organic molecules, which are very resistant to degradation, increase (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 originating from primary production. In dark marine caves, chlorophyll is short-lived and rapidly degrades to phaeophytin. Thus, high values of this ratio will characterize ‘fresh’ vegetal organic matter, rich in live phytoplankton cells, while lower values will indicate detrital vegetal matter (Fichez 1990c). Between the semidark 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 primary consumers inwards (Bianchi et al. 2003).

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 (including decomposing organisms which died inside the cave), and resistance to starvation, which allows survival under an irregular and unpredictable food intake (Bibiloni et al. 1984, Culver 1985). In addition, there are also strategies that implicate the functioning of the entire cave ecosystem, rather than the physiological response of individual species. Bianchi et al. (2003)

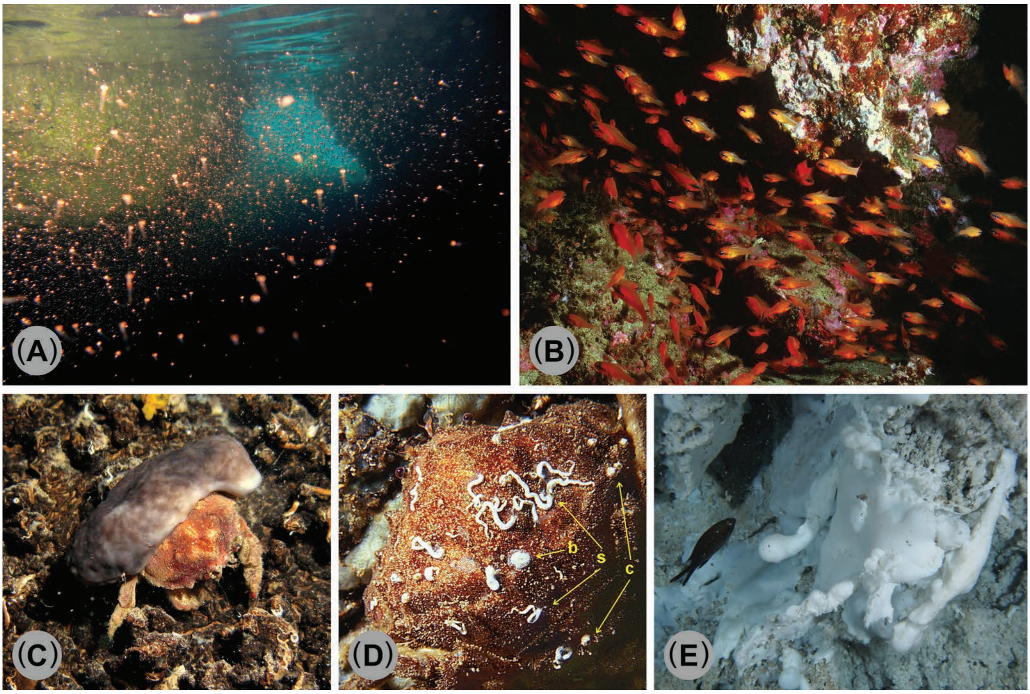

Figure 24 Main strategies to mitigate trophic depletion in Mediterranean marine caves: (A) swarm-forming mysids and (B) the cardinal fish *Apogon imberbis*, which perform nychthemeral (day–night) migrations; (C) *Dromia personata* is called 'sponge crab' due to its habit to carry the sponge *Chondrosia reniformis* on its carapace for camouflage, while the carapace of old individuals (D) may also be settled by small sessile epibionts (b=bryozoans; c=cirripeds; s=serpulids), which are therefore allowed foraging outside the cave and dispersing their propagules (epibiosis and phoresy); (E) foam-like microbial structures providing potential trophic sources for consumers such as the fish *Chromis chromis* (chemo-litho-autotrophy). Photos by V. Gerovasileiou (A and C), C.N. Bianchi (B and D) and T. Dailianis (E).

identified three principal mechanisms: diel migrations (Figure 24A and B), epibiosis and phoresy (Figure 24C and D), and chemo-litho-autotrophy (Figure 24E).

Diel migrations Motile species exhibiting diel migration patterns significantly affect the flow of energy in the marine cave ecosystem since they mitigate oligotrophy by importing organic matter. Some stygoxene species of crustaceans and fishes find shelter within caves during daytime but forage outside the cave at night. This role has been studied mostly in swarm-forming mysids (Figure 24A) and in the cardinal fish *Apogon imberbis* (Figure 24B) (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, *H. margalefi* swarms have thousands of individuals, while *H. lamornae mediterranea* can congregate in 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 (Coma et al. 1997, Rastorgueff et al. 2011). They can also be preyed on 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), among others. The cardinal fish *Apogon imberbis*, which is the most abundant (up to 1800 individuals per 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. This fish shelters inside caves during the day but feeds on small invertebrates (e.g. crustaceans and annelids) in rocky beds and *Posidonia* meadows at night.

Epibiosis and phoresy Large decapod crustaceans that move between the cave and the external marine environment create an opportunity for transport (phoresy) of 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*) (Figure 24C). The crab picks the sponge fragments up just for camouflage, but the sponge regenerates rapidly, survives for long periods on the crab, and can reproduce both sexually and asexually (McLay 1983, Voultsiadou-Koukoura & Koukouras 1993). Many small sessile taxa, such as serpulids, bryozoans and barnacles, can settle as epibionts on the carapace of old individuals of *Dromia personata* (Figure 24D). These sessile suspension-feeders, thanks to the phoretic transport, are able to feed outside at night, thus bypassing the hydrological confinement gradient and avoiding the trophic depletion conditions inside caves. These epibionts, besides participating in the horizontal transfer of organic matter, can represent a source of larvae capable of maintaining pseudo-populations of stygophilic taxa in caves, thus contributing to their biodiversity (Bianchi et al. 2003).

Chemo-litho-autotrophy Explorations at Cape Palinuro, Tyrrhenian Sea, brought to light caves with sulphidic hydrothermal springs (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 the cave. At the interface between the marine water layer and the hydrothermal waters, a permanent chemocline is formed (Figure 25). The vault of the cave is populated by well-adapted prokaryotes (*Beggiatoa*-like bacteria), which form extensive mats and are responsible for oxidizing sulphides to sulphates (Mattison et al. 1998, Canganella et al. 2002, 2007). From this oxidation, sulphur bacteria draw energy for their metabolism, which is therefore 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).

The profound influence that the sulphur bacterial production has on the marine cave ecosystem has mostly been studied in the Grotta Azzurra of Cape Palinuro (Tyrrhenian Sea, 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 (Figure 26) (Abbiati et al. 1992, Bianchi et al. 1994, Cinelli et al. 1994, Southward et al. 1996, Airoldi & Cinelli 1997). Some species of sessile suspension-feeders, such as the sponge *Geodia cydonium* and the scleractinian *Astroides calycularis*, exhibit gigantism, which is probably

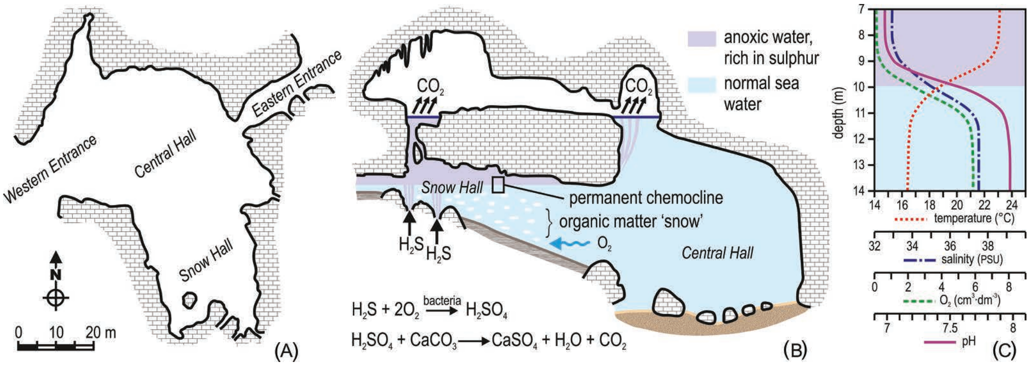

Figure 25 Sulphur-bacterial metabolism in the so-called ‘Sala della Neve’ (= Snow Hall) of the Grotta Azzurra of Cape Palinuro, Italy. (A) Plan view of the cave, with main cave zones indicated; (B) transverse section across the tunnel-shaped Central Hall (to the right) and the blind-ended Snow Hall (to the left), and hypothetical scheme of the sulphur chemistry; (C) vertical profiles of selected hydrological parameter across the chemocline. Redrawn and modified from Bianchi et al. (1996, 1998, 2003).

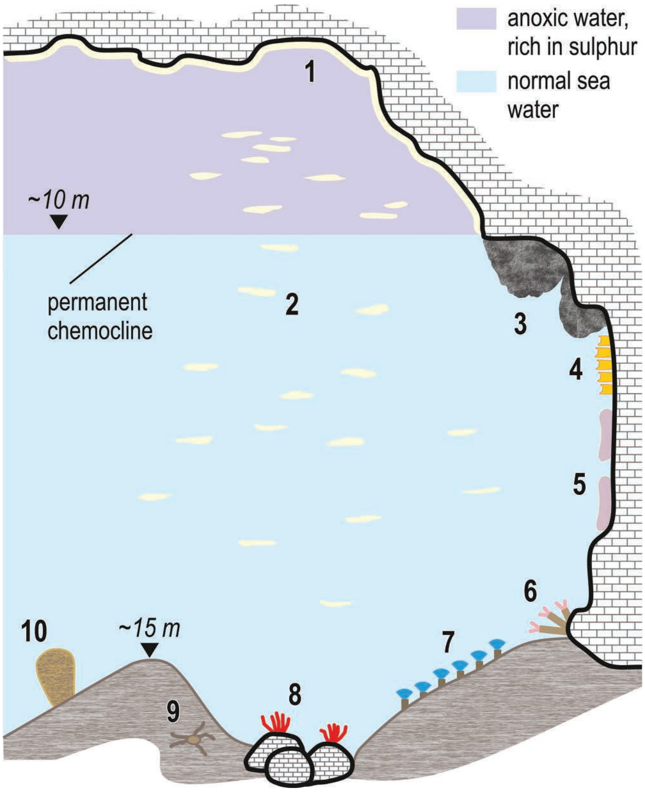

Figure 26 Biological sketch of the so-called ‘Sala della Neve’ (= Snow Hall) of the Grotta Azzurra of Cape Palinuro, Italy. 1: Sulphur-bacterial mat; 2: flakes of organic matter of bacterial origin; 3: *Geodia cydonium*; 4: *Leptopsammia pruvoti*; 5: *Petrosia ficiformis*; 6: *Phyllochaetopterus socialis*; 7: *Sabella pavonina*; 8: *Antedon mediterranea*; 9: *Ophioderma longicaudum*; and 10: *Pinna nobilis*. Redrawn and modified from Bianchi & Morri (2003).

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*, ‘garden’ 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 into the anoxic waters above, to graze on sulphur bacterial filaments. The consumers dwelling on the cave floor, which are either suspension-feeders (e.g. the polychaete *Sabella pavonina*, the bivalve *Pinna nobilis* and the crinoid *Antedon mediterranea*) or detritivores (e.g. the ophiuroid *Ophioderma longicaudum*), also take advantage of the ‘snow’ of bacterial organic matter that falls from the ceiling in the form of white flakes, which is the origin of the name ‘Sala della Neve’ (= Snow Hall) given to this part of the Grotta Azzurra (Bianchi et al. 2003).

During a recent study on the marine cave biodiversity of the National Marine Park of Zakynthos Island (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 organisms, that were characterized 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 by V. Gerovasileiou, some fishes (e.g. *Chromis chromis*) were apparently feeding on white microbial aggregates advected by the excurrent water flowing from cavities and fissures (Figure 24E). Further study is required in order to investigate the trophic structure and function of these ecosystems, which are probably more widespread than previously thought.

Analogies with deep-sea ecosystems

Apart from few exceptions, the export of organic matter from marine caves to external environments is normally negligible, as are the sedimentation losses. Virtually all of the organic material present in marine caves is processed and remineralized through aerobic processes, with high efficiency (Fichez 1990b, 1991a,c, Bianchi et al. 1996). Fichez (1991a) measured benthic oxygen uptake and carbon cycling in the Grotte des Trémies (Marseille region, France) and found that while in the outer semidark 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 the degradation of organic carbon occurred only through aerobic processes (Figure 27).

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). These characteristics make 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 shallow habitats due to drifting or gravity (Bianchi et al. 2003).

In those marine caves that have sulphur springs, the dependence of their ecosystem on chemo-litho-autotrophic production recalls ecosystems that exist at great depth near 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

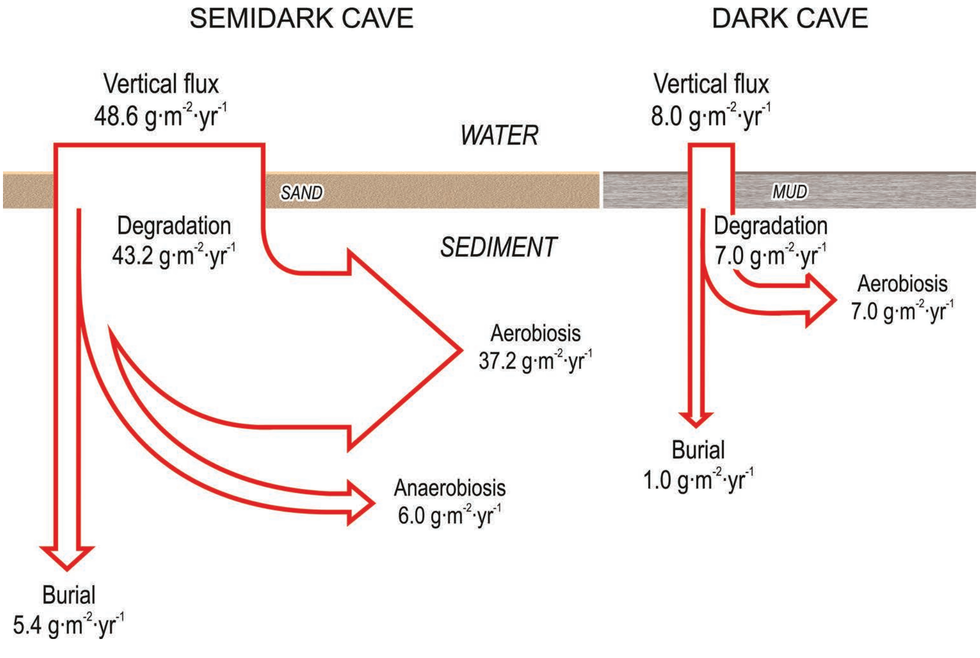

Figure 27 Organic carbon cycle at the water–sediment interface in the semidark and dark sections of the Grotte des Trémies (Marseille region, France). Organic carbon fluxes are expressed in g·m^{-2}·yr^{-1}, arrow width being roughly proportional to the amount of carbon flux. Redrawn and modified from Fichez (1991a).

patinas and nodules (Figure 8A), essentially iron and manganese oxides, which give blackish colour to the rocks and walls of the more confined dark sections of submerged caves (Laborel & Vacelet 1958, Bianchi et al. 1986, Allouc & Harmelin 2001). Their formation probably relates to bacterial metabolism, under particular physical–chemical conditions that 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 (Harmelin & Vacelet 1997), which occupy over half the surface of our planet.

Trophic organization

Theoretical models on the trophic organization of Mediterranean marine cave ecosystems have been developed by Ott & Svoboda (1978), Russo & Bianchi (2003) and Rastorgueff et al. (2015a). Organic matter supply in marine caves consists principally of particulate organic matter (POM), which is usually a mixture of phytoplankton, land-derived and anthropogenic material carried to the sea by river run-off, and sewage outflow or even matter percolating through the cracks and fissures of bedrock (Rastorgueff et al. 2011, 2015a). A further contribution comes from motile organisms (i.e. crustaceans and fishes) which move outside–inside caves, on either a diel or occasional basis, leaving their faecal pellets or their remains (Figure 28).

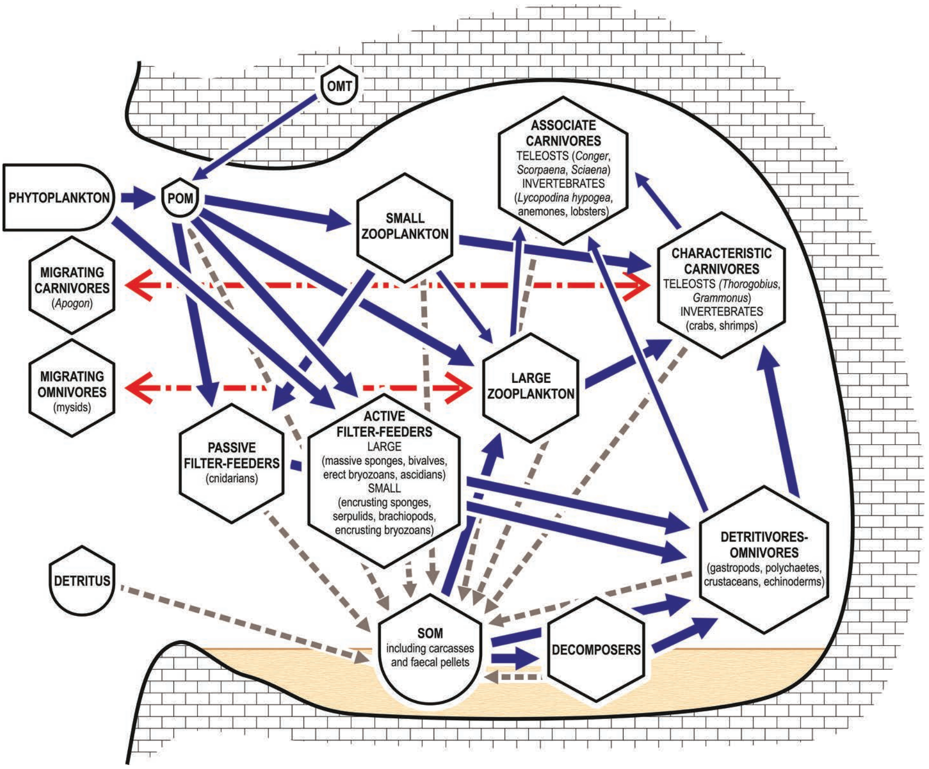

Figure 28 A simplified model of the structure and functioning of the Mediterranean marine cave ecosystem. Solid arrows denote organic matter fluxes, their thickness being roughly indicative of the assumed intensity of the fluxes. Dashed arrows represent the detrital organic matter reaching the cave floor. Horizontal dash-dotted arrows indicate nychthemeral horizontal migration of mysids and the cardinal fish *Apogon imberbis*, which may input organic matter into the cave. OMT: organic matter of terrestrial origin; POM: particulate organic matter; SOM: sedimentary organic matter. Redrawn and modified from Ott & Svoboda (1978), Russo & Bianchi (2003) and Rastorgueff et al. (2015a).

As primary producers are generally absent from inside marine caves, the major trophic-behavioural categories (Ott & Svoboda 1978, Russo & Bianchi 2003, Rastorgueff et al. 2015a) are the secondary producers (passive and active suspension-feeders), the consumers (characteristic and associate carnivores), the detritus-feeders and omnivores, the migrants and the decomposers.

Secondary producers

These are sessile animals that live by drawing directly from the organic matter imported from outside. They are suspension-feeders, either passive (e.g. cnidarians) or active (e.g. 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 (Shimeta & Jumars 1991). Passive suspension-feeders require a higher water flow, providing nutritive particles, and thus, they are more abundant at the cave entrance and cave sections 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 sections is limited by water confinement, except for tunnel-shaped caves (Bianchi & Morri 1994). Active suspension-feeders are the most common and widespread taxa inside marine caves as they are comparatively 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. 2017b). The dominance of particular growth forms in distinct cave sections 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 sections is related to the fact that they present a more effective filtration surface/volume ratio, and thus, they can exploit the sparse particulate organic matter of the water (Bibiloni et al. 1989). All in all, secondary producers constitute the main trophic level in terms of both biomass and species richness in Mediterranean marine caves and represent the trophic substratum necessary for higher order consumers (Figure 29).

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 from the nearby algal-dominated communities can frequently be observed grazing on plant detritus accumulated on the cave floor (Harmelin et al. 1985, Russo & Bianchi 2003). The carnivores to be found in caves include both

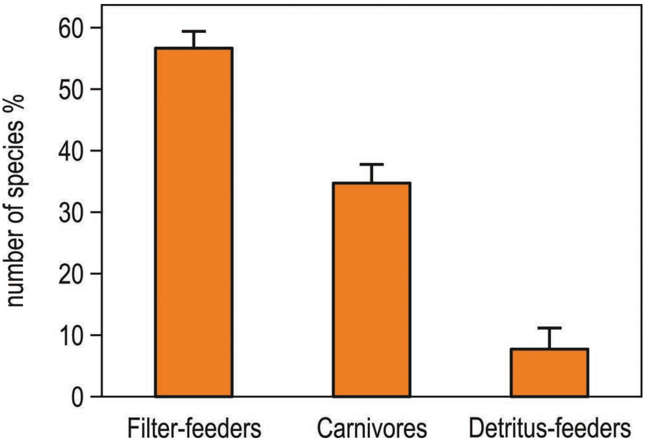

Figure 29 Qualitative dominance of trophic guilds in the polychaete assemblages of three blind-ended caves of the Sorrentine Peninsula, Italy. Redrawn and modified from Bianchi (1985).

motile and sessile forms. Motile carnivores, either stygophiles or stygoxenes, can be further categorized into characteristic carnivores, which are frequently observed in caves, although they also occur in other 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*, *L. nilita*, *Palaemon serratus*, *Plesionika narval* and *Stenopus spinosus*). The associate carnivore category also includes fish species (e.g. *Conger conger* and *Phycis phycis*) and decapods (e.g. *Homarus gammarus*, *Palinurus elephas* and *Scyllarides latus*). Associate carnivores also include sessile species such as the cladhorizid sponge *Lycopodina hypogea*, the sea anemone *Halcampoides purpureus* and ceriantids (e.g. *Arachnanthus oligopodus* and *Cerianthus membranaceus*), which prey on populations of small motile taxa, such as mysids (Russo & Bianchi 2003, Rastorgueff et al. 2011, 2015a,b).

Regarding macroinfauna, the study of the gut content of soft substratum 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 reason behind this absence remains uncertain but could be possibly linked to physical gradients that could act as a limiting factor for the presence of detritivores or even to change of feeding behaviour under poor trophic conditions (Navarro-Barranco et al. 2013b and references therein). 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. (2016c) showed that carnivores (mainly crustaceans) dominated in terms of abundance in both sponges (especially the amphipod *Colomastix pusilla*). While carnivores dominated in terms of species richness in *Aplysina aerophoba*, deposit-feeders (mainly polychaetes) were the most species-rich feeding group in *Agelas oroides*. The trophic structure of the sponge-associated macrofauna did not change significantly across different cave sections.

Detritus-feeders and omnivores

Animals that feed on sedimented detritus, and omnivores, constitute an important component of the food chain in the marine cave ecosystem, as they make the organic matter 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 crustaceans (among which the decapods *Herbstia condyliata*, *Galathea strigosa* and *Scyllarus arctus*), gastropods, motile polychaetes and echinoderms. Large individuals of the brittle star *Ophioderma longicaudum* were found to be unusually abundant in the ‘Snow Hall’ of the Grotta Azzurra (Tyrrhenian Sea, Italy) and feeding on the ‘flakes’ of organic matter of bacterial chemosynthetic origin (Bianchi et al. 1994, Bianchi & Morri, 2003).

Migrants

In addition to swarm-forming mysids and the cardinal fish *Apogon imberbis*, other motile species, either characteristic or associate carnivores, go feeding outside at night. Examples include decapod crustaceans (e.g. *Plesionika narval*, *Palinurus elephas*, *Scyllarus arctus*, *Homarus gammarus*), cephalopods (e.g. *Octopus* spp.) and fishes (e.g. *Phycis phycis*, *Sciaena umbra*, serranids, sparids, gobies). The presence of such migrant populations, sometimes in high abundance, can represent a significant 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). It is not known if these species can also represent an energy loss for the cave system.

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).

Other biotic interactions

Spatial interspecific competition

The strong environmental gradients that 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 implies that the cave ecosystem sustains a high degree of functional redundancy, thus maintaining important ecosystem processes (Gerovasileiou et al. 2017b). The dispersal of propagules from their parental habitats (inside or outside caves) is determined not only by environmental parameters (e.g. water movement) but also by larval behaviour (e.g. swimming efficiency and phototaxis), by phoresy 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 sections and microhabitats), where species compete for the limited available resources (Gerovasileiou et al. 2017b). 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 semidark cave zone: sciaphilic sessile animals are competitively inferior to macroalgae, but become dominant where the reduction in light levels leads to the disappearance of the latter (Pérès & Picard 1949, Riedl 1966, Cinelli et al. 1977, Balduzzi et al. 1989, Corriero et al. 2000, Martí et al. 2004a, Gerovasileiou et al. 2017b).

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 (Spain) and found that sciaphilic and cryptic communities (i.e. the lower side of coralligenous blocks and semidark 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, Spain (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 tunicates studied 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 in spring. However, the highest number of bioactive sponges was found in the semidark cave community. The higher number of non-bioactive sponges in the dark cave community is possibly related to the fact that there are less interspecific 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 either a trade-off in the allocation of energy for chemical defence and for three-dimensional growth, or that it is otherwise easier for an encrusting species to be overgrown, so it needs a stronger defence. Chemical bioactivity seemed to protect species from interspecific contact. Furthermore, toxic species generally lacked epibionts.

Santonja et al. (2018) conducted chemosensory experimental assays and found that cave-dwelling crustaceans (i.e. *Hemimysis margalefi* and *Palaemon serratus*) avoided seawater containing the chemical extracts of four sponges that are commonly found at the entrance of Mediterranean marine caves (i.e. *Aplysina cavernicola*, *Haliclona fulva*, *Oscarella tuberculata* and *Spongia officinalis*), probably due to the deterrent or toxic properties of specialized metabolites present in the sponges. On the other hand, the same cave-dwelling crustaceans were attracted by cave seawater and seawater conditioned with the sponge assemblage – in contrast to crustaceans from other habitat types – suggesting that chemical cues produced by sponges at the cave entrance could potentially guide cave-dwelling crustaceans to the entrance of caves during their diel horizontal migrations.

Therefore, chemical bioactivity of benthic invertebrates has an important role in the structuring and functioning of marine cave communities that deserves further investigation.

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. 2017b): ‘habitat formers’ provide habitat via their own living body; ‘constructors’ build structures with their mineral skeletons; ‘binders’ agglomerate and expand the components of the habitat framework; whereas ‘borers’ actively penetrate hard substrata via their bio-eroding activity.

Erect (arborescent or tubular) and massive sponges, anthozoans, bryozoans and other sessile taxa are habitat formers that create an upper layer which increases the three-dimensional complexity of benthic communities and support assemblages of epibionts and associated macroinfauna. Navarro-Barranco et al. (2015) studied the species composition of amphipod assemblages associated with six taxa, 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 *Astroides 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, 2016c). The study of the macrofauna associated with the habitat-forming sponges *Agelas oroides* and *Aplysina aerophoba* in two marine caves of Lesvos Island (Aegean Sea, Greece), revealed a rich fauna comprising 86 taxa (Gerovasileiou et al. 2016c). Crustaceans dominated in terms of abundance while polychaetes were the most species rich group. Although total species richness decreased from the entrance to the innermost dark cave sections, mean density and diversity did not vary significantly, suggesting that sponges maintain their functional role as habitat formers (also characterized as ‘living hotels’ by Pearse 1950) throughout the caves by increasing habitat complexity in the impoverished inner dark cave.

Constructors are represented by several invertebrate taxa with hard body parts, skeletons or tubes, such as serpulid polychaetes, scleractinians, bryozoans, bivalves and brachiopods (Gerovasileiou et al. 2017b). The serpulid *Protula tubularia* often forms aggregates which provide the basis for the creation of ‘biostalactites’. Sponges, bryozoans, foraminiferans (e.g. *Miniacina miniacea* and *Rhizonubecula adherens*) and carbonate-forming microbes also take part in the bioconstruction process (Belmonte et al. 2009, 2020, Sanfilippo et al. 2015, 2017, Guido et al. 2016a,b, 2017a,b, 2019a,b, Rosso et al. 2021). To date, biostalactites have been discovered in dark caves of Apulia (Onorato et al. 2003, Belmonte et al. 2009, 2020, Rosso et al. 2021), Sicily (Guido et al. 2012, 2013, Sanfilippo et al. 2015) and other Italian localities (Ingrosso et al. 2018), Cyprus (Guido et al. 2017a, Jimenez et al. 2019) and Greece (Sanfilippo et al. 2017, Guido et al. 2019a,b). Another characteristic bioconstruction has the shape of small nodules and subparallel crests (approximately 2–3 cm in height), which may develop in the transitional zone between the semidark and dark cave biocoenoses, and sometimes further inside the dark cave zones (Harmelin 1985, 2000, Harmelin et al. 1985, Rosso et al. 2013a, 2015). These bioconstructions result from the concretion of several bryozoan colonies (e.g. *Onychocella marioni* and *Hippaliosina depressa* – the latter mainly in the eastern Mediterranean Sea) and other encrusting taxa (e.g. agglutinated foraminiferans, corals, serpulids and brachiopods), thus creating microstratification and a low-profile vertical structure (Harmelin et al. 1985, Rosso et al. 2019). They have been reported from marine caves near Marseille (Harmelin 1985, 2000, Harmelin et al. 2003), Sicily (Rosso et al. 2013a, 2015) and Greek islands in the Aegean and Ionian seas (Rosso et al. 2019, V. Gerovasileiou, unpublished data), those of the latter regions being smaller in size as compared to those of Marseille region. The brachiopods *Novocrania anomala* and *N. turbinata* sometimes participate into bioconstructions (Logan et al. 2004, Radolović et al. 2015, Bitner & Gerovasileiou 2021). In general, the size of the bioconstructions ranges from a few centimetres for bryozoan nodules up to 2 m for biostalactites (Onorato et al. 2003, Guido et al. 2017a, Jimenez et al. 2019, Rosso et al. 2021).

Sponges exhibit a wide variety of ecosystem engineering activities in cave ecosystems (Gerovasileiou & Voultsiadou 2012, Gerovasileiou et al. 2017b). In addition to the habitat-forming species, several others act as binders, agglomerating carbonate particles and 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. 2017b).

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. 2017b). Borers penetrate actively calcareous substrata, including biogenic ones, thus creating an endolithic layer (Riedl 1966). The large amount of sponges in marine caves of Lesvos Island (Aegean Sea, Greece), and particularly of endolithic and insinuating species, was suggested to induce competition with carbonatogenetic bacteria for the same living cryptic spaces, thus preventing the development of microbialites, which are otherwise abundant in the microcavities of large biostalactites in caves of Italy and Cyprus (Guido et al. 2019a,b).

Dynamics and 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 substrata under dark conditions in two marine caves of the Marseille region (France): the blind-ended Trémies cave and the tunnel-shaped Moyade cave. While in the tunnel-shaped cave, 9–10 years were sufficient for colonized plates to reach a 'mature' state, with 100% of the substratum 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 have low ecological resilience.

The study of recruitment, settlement and primary succession of sessile benthos in the shallow, semi-submerged cave Grotta di Ciolo (Salento Peninsula, Italy), using baked clay panels, showed that while a two-year recruitment period allowed for a complete colonization of panels at the entrance zone, recruitment was very slow in the intermediate and inner dark zones, where the natural benthic communities of the cave walls were not replicated on panels (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 substratum 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 small seasonal variation in community structure 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 substratum 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 neither the artificial panels nor the natural substratum of vertical cave walls was explicable on the basis of seasonality. The study of benthic foraminiferans in two marine caves of Sardinia showed a marked reduction in foraminiferan abundance, or even disappearance, between August 2014 and April 2015, probably because of the strong freshwater flows that occurred during the rainy season, which caused the removal of superficial sediment layers (Romano et al. 2020).

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 (north-western Mediterranean) represents a partial exception, as historical data are available for a few caves (Bianchi et al. 2019). For instance, the sponge fauna of two semi-submerged caves was first studied in 1961–1963 (Sarà 1964) and again in 2015–2016 (Nepote et al. 2016, Costa et al. 2018). Between these studies, there was an increase in species richness and a significant change of growth forms, with massive sponges having been replaced by encrusting forms. Similar results were 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 heatwaves of 1999 and 2003 (Bianchi et al. 2019). 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*), followed by 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 lies between the sea surface and 7 m depth, is relatively short (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 freshwater infiltration – salinity (Bianchi et al. 1986). Cluster analysis of physical-chemical data, namely water temperature (°C), salinity (PSU), relative density (σ), water movement ($cm{\cdot}s^{-1}$), light ($\mu W{\cdot}cm^{-2}$), pH, dissolved oxygen (ppm and % saturation), organic suspended matter ($mg{\cdot}L^{-1}$ and % of total suspended matter), C/N ratio, chlorophyll *a* ($\mu g{\cdot}L^{-1}$), sediment mean grain size (mm), and % of fine (<0.25 mm) sediment, allowed four zones to be recognized: outer cave, main hall, shaft, and inner 'lakes' (Morri et al. 1994a). Each zone had its own biological assemblage. The outer cave was inhabited by associations of sciaphilic algae but also by typical facies of the semidark biocoenosis (Laborel 1960, Pérès & Picard, 1964), characterized by sponges, large hydroids and the anthozoan *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 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 *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. The motile fauna included the crustaceans

Herbstia condyliata, *Lysmata seticaudata* and *Stenopus spinosus* and the fishes *Apogon imberbis*, *Grammomus ater*, *Sciaena umbra* and *Thorogobius ephippiatus*. 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*) and by the shrimp *Palaemon serratus* (Figure 8B).

The above situation remained apparently stable for about two decades. However, increased seawater temperature since the 1990s induced the substitution of the cold-water mysid *Hemimysis speluncola* by the warm-water congener *H. margalefi* (Chevaldonné & Lejeusne 2003). Such a species shift is likely to exert great influence on the energy budget of cave ecosystems (Bianchi 2007): *H. speluncola* typically forms huge swarms, while *H. margalefi* only occurs in small groups, implying a lesser role for *H. margalefi* in organic matter import from outside. Changes in the sessile assemblages led to a general homogenization of the cave communities, and the four biotic zones characterizing the cave were less distinct.

Thanks to the availability of a 30-year-long series of quantitative data (substratum cover from photo-quadrats) 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 over the years 1986 to 2013 (Figure 30A),

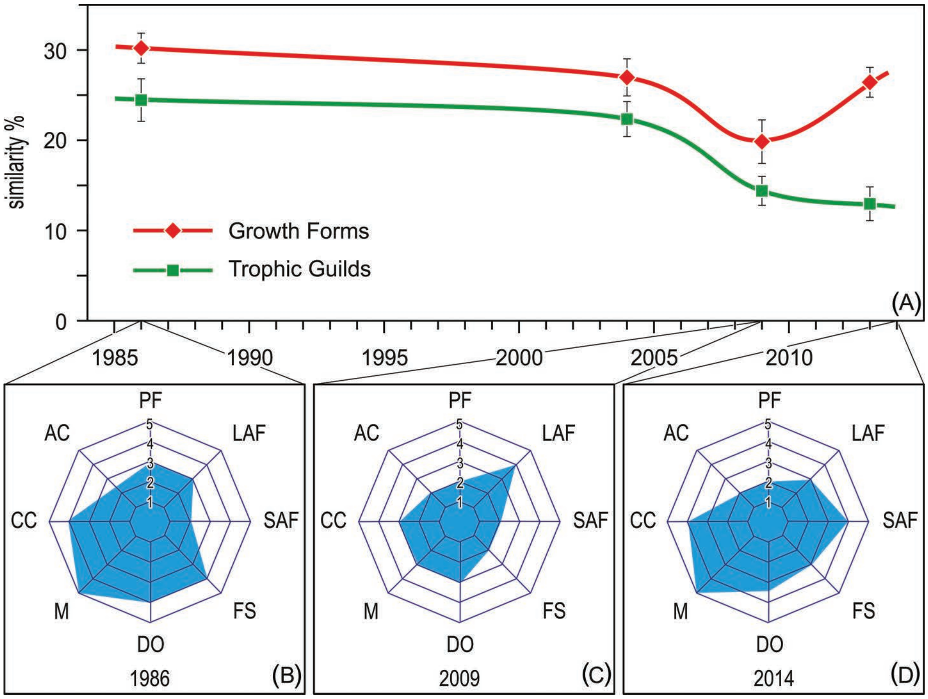

Figure 30 Changes with time in the biota of the Grotta Marina of Bergeggi (Italy). (A) Trends of average (± standard error) Bray–Curtis similarity between all the photographic samples of a given year and the 1986 centroid using non-taxonomic descriptors of the sessile assemblages: growth forms exemplify ecosystem structure, and trophic guilds represent ecosystem functioning. (B–D) Ecological quality of Bergeggi Cave in different years using the CavEBQI approach (Rastorgueff et al. 2015a), which adopts a semiquantitative scale 1–5 for eight ecological groups. PF: passive filter-feeders; LAF: large active filter-feeders; SAF: small active filter-feeders; FS: filter-feeders stratification; DO: detritus-feeders and omnivores; M: mysids; CC: characteristic carnivores; AC: associate carnivores. Redrawn and modified from Rastorgueff et al. (2015a) and Montefalcone et al. (2018).

coinciding with major local disturbances from coastal developments. The ecological quality of the cave, estimated through the ecosystem approach of Rastorgueff et al. (2015a), also underwent change (Figure 30B). Ecological group composition and 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 building 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-shaped cave Túnel del Dofí, a popular scuba diving spot in the Medes Islands (Catalonia), revealed significant changes in benthic community structure (composition and abundance). Three-dimensional growth forms (e.g. the red coral *Corallium rubrum* and the bryozoans *Scrupocellaria* sp. and *Reteporella grimaldii*) decreased in abundance, with a concomitant increase in the abundance of encrusting sponges. The areal extent of air-pockets on the ceilings, from the air exhaled by scuba divers, increased from 0.7% in 1978 to 9.07% in 2016 (Burgués et al. 2016).

The study of sessile benthos in Cerro-Gordo submerged cave (Granada, Spain), over a decade (2007–2016), 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 outer and inner cave sections (Sempere-Valverde et al. 2019). During the timeframe examined, sponge cover decreased, while that of polychaetes and brachiopods increased, especially in the inner dark section. In the semidark cave section, 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 southern sections) is a major impediment to the monitoring and evaluation of potential impacts and changes in their ecological status (Gerovasileiou et al. 2016b, 2017a, Sempere-Valverde et al. 2019).

Conservation value and current threats

Conservation value

Marine caves are acknowledged as 'biodiversity reservoirs' and 'refuge habitats' of great conservation value, as they harbour a rich biodiversity (32–71% of the Mediterranean sponge, anthozoan, bryozoan, tardigrade and brachiopod species) that includes 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, Ouerghi et al. 2019). Among the most emblematic and charismatic species inhabiting marine caves are the Mediterranean monk seal *Monachus monachus* (Figure 31A) and the red coral *Corallium rubrum* (Figure 31B), both listed as endangered (EN) in the IUCN Red List of Threatened Species.

The survival of important monk seal populations in the north-eastern Mediterranean, especially in the Aegean Sea, is linked to the availability of high numbers of suitable cave habitats across the coasts and insular locations of the region (Voultsiadou et al. 2013) coupled with 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 its survival.

The red coral has been traditionally considered a typical species of the semidark 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 in caves of Marseille region and Corsica (Garrabou et al. 2001, 2017).

Figure 31 Two of the most charismatic protected species in Mediterranean marine caves: (A) a group of Mediterranean monk seals, *Monachus monachus*, resting in a marine cave in the Aegean Sea, Greece (on the left an adult female with her two-month-old pup); (B) the red coral *Corallium rubrum* on the ceiling at the entrance of the Marcante cave, Portofino, Italy. Photos by P. Dendrinos (A) and C.N. Bianchi (B).

Several other protected species listed in Annexes II (list of endangered or threatened species) and III (list of species whose exploitation is regulated) 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 *Naria spurca* (Figure 5I) and *Luria lurida*, the date mussel *Lithophaga lithophaga*, the hatpin urchin *Centrostephanus longispinus*, the slipper lobster *Scyllarides latus* (Figure 11E) and the brown meagre *Sciaena umbra*. In addition, all protected sponges are also found in caves, including the deep-water species *Lycopodina hypogea*, first described from the famous 3PP Cave of Marseille region (Vacelet & Boury-Esnault 1996), and typical cave-dwelling species, such as the relict calcareous sponge *Petrobiona massiliana* (Figure 5B) 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 (Gerovasileiou & Voultsiadou 2012, Manconi et al. 2013, Padiglia et al. 2018).

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), even though future research might show that some could be also distributed in other cryptic or deep-sea habitats. Thus, marine caves have been considered as 'natural laboratories' or 'deep-sea mesocosms' in the littoral zone because they provide direct human access to bathyal-like conditions within reach of scuba divers (Harmelin & Vacelet 1997). 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 concerns not only sessile taxa, but also motile fauna, such as the rare gobids *Corcyrogobius liechtensteini*, *Didogobius splechtnai*, *Gammogobius steinitzi* and *Speleogobius trigloides*, which live in marine caves and other cryptic habitats (Bussotti et al. 2015 and references therein, Ragkousis et al. 2021).

The presence of caves in rocky coasts may provide additional resources for fishes (e.g. 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 that 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 have raised biotechnological interest in cave biota (e.g. sessile taxa and microbial mats) as potential sources of bioactive substances (Uriz et al. 1991, Martí et al. 2005, Turon et al. 2009, Audoin et al. 2013) and for bioenergy and bioremediation (Polymenakou et al. 2018).

The high and unique biodiversity of marine caves, coupled with their geomorphological complexity and high aesthetic value, make them popular locations for marine-based recreational activities (Rovere et al. 2011, Salomidi et al. 2012), such as boat tours, snorkelling and scuba diving throughout the Mediterranean Sea. In addition, some marine caves are interesting from paleontological, archeological and paleo-climatological perspectives (e.g. Antonioli et al. 2001, Poulakakis et al. 2002, Collina-Girard 2004, Galanidou et al. 2020). Notable examples include the famous Grotte Cosquer in the Marseille region and the Elephant's Cave in Crete.

The examination of a biostalactite collected in the 'lu Lampiùne' marine cave in Italy (Apulia) showed that its accretion started ca. 6000 years ago with a rapid growth of large-sized serpulids (*Protula*), and then decreased ca. 3000–4000 years ago, reflecting a shift in main bioconstructors, probably caused by environmental changes (Belmonte et al. 2020, Rosso et al. 2021 and references therein). Other examples of unique bioconstructions include large sponge masses of the lithistid *Neophrissospongia endoumensis* recently found in marine caves of Crete (Greece) by Pisera & Gerovasileiou (2021) that could be approximately 769–909 years old in the case of the largest specimen observed (about 100 cm across). The occurrence of such slow-growing formations highlights the urgent need for appropriate management and conservation actions.

For all the foregoing reasons, marine caves are listed for protection 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', which also integrates semidark cave communities (Ballesteros et al. 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 (Pergent et al. 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). Despite designations and conservation action plans, according to a preliminary comparison of different protocols for marine cave visitation worldwide, in most countries no specific regulations or management plans are implemented (Petricioli et al. 2015). Surprisingly, few MPAs have set specific limitations regarding the maximum number of divers or have required permits for visiting caves. The large number of marine caves in coastal areas with extensive rocky outcrops, coupled with the lack of detailed mapping and monitoring initiatives, hinders the effective conservation and management of these unique ecosystems and the evaluation of potential impacts on cave biota. Therefore, marine caves are currently exposed to numerous threats and impacts.

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 innermost parts of 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, the present seawater warming being mostly of anthropogenic origin (Bianchi 2007), cause important changes to both the motile and sessile components of cave communities (Chevaldonné & Lejeusne 2003, Parravicini et al. 2010, Costa et al. 2018, Sempere-Valverde et al. 2019).

Despite difficult access to caves, 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. of *Sciaena umbra* and *Phycis phycis*), urbanization and building of coastal structures, waste outflows, littering (Figure 8D), 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). Several sessile invertebrates with erect morphologies, as well as their bioconstructions, are slow-growing, fragile, and thus highly vulnerable to mechanical damage caused by divers colliding unintentionally with them, which is more likely to happen inside caves and beneath overhangs than elsewhere. Typical examples are the anthozoans *Astroides calycularis*, *Leptopsammia pruvoti*, *Parazoanthus axinellae* and *Corallium rubrum*, and the erect and fragile bryozoans *Myriapora truncata* and *Reteporella* spp. (Figure 32)

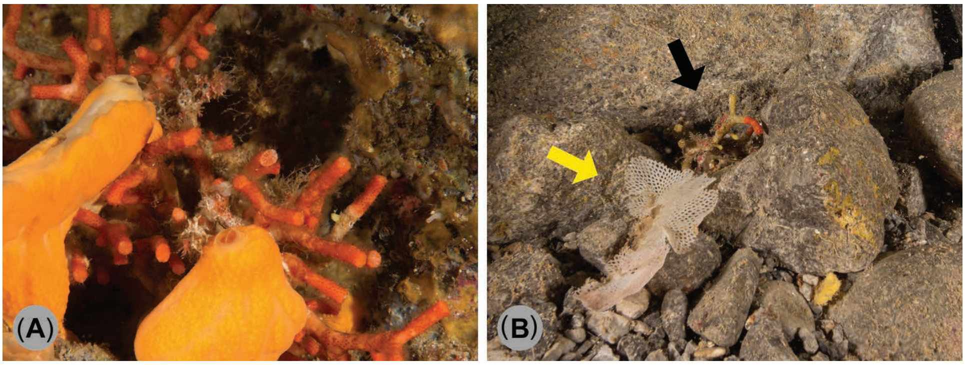

Figure 32 Erect bryozoans are fragile and vulnerable to mechanical damages: (A) the 'false coral' *Myriapora truncata* is a typical dweller of cave walls and ceilings; (B) fallen fragments of the branching species *M. truncata* (black arrow) and *Reteporella* sp. (yellow arrow) on a rocky cave floor, detached from the walls and ceilings either naturally or due to contact with divers. Photos by T. Dailianis.

(Milazzo et al. 2002). The comparison of benthic assemblages of three marine caves from the MPA of Capo Caccia (Sardinia, Italy), characterized by different intensities of diving tourism, showed that organisms with erect calcareous skeletons are the most vulnerable to diving activities and that the quantity of skeletons and skeletal fragments in cave bottom sediments is a good indicator of the level of diving impact (Scinto et al. 2010). Di Franco et al. (2009) evaluated diver behaviour in seven types of subtidal habitats in Capo Gallo-Isola delle Femmine MPA in Sicily and found that the highest rates of total and unintentional contacts occurred in caves (in particular by divers with higher certification levels). The anthozoans *Eunicella singularis* and *Astroides calycularis* were the species most frequently damaged by divers. Guarnieri et al. (2012) examined the effect of recreational diving on four marine caves in MPA of Capo Caccia-Isola Piana (Sardinia, Italy) where diving activities are regulated and found that organisms with vertical growth and rigid body structure (e.g. *Lithophyllum stictiforme*, *Reteporella grimaldii* and *Idmidronea triforis*) were significantly more abundant and homogeneously distributed in a fully protected cave than in the visited ones. Sediment resuspension and accumulation of exhaled air bubbles at the cave ceiling can also have detrimental effects on sessile suspension-feeders (Milazzo et al. 2002, Lloret et al. 2006, Di Franco et al. 2010, Burgués et al. 2016). Coastal structures (e.g. jetties, breakwaters, groynes) alter sediment transport and may cause increased sediment deposition in the innermost parts of caves (Figure 8C), with consequent smothering 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 spread of non-indigenous species, especially in the eastern and southern regions. A total of 56 non-indigenous species (NIS) and cryptogenic taxa have been reported so far from approximately 50 marine caves and tunnels of the Mediterranean (Gerovasileiou et al. 2016b), including molluscs (15), cnidarians (9), bryozoans (7), polychaetes (6), crustaceans (6), macroalgae (3), fish (3) and tunicates (2). Most of these taxa (66%) were found in caves of the south-eastern Levantine Sea (mainly in Lebanon: Zenetos et al. 2015), with shipping and Lessepsian migration through Suez Canal being their main pathways of introduction (Figure 33). These taxa were mostly reported from the entrance and semidark 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 marine caves of the Levantine and southern Aegean seas, and the population explosion of non-indigenous fishes, for instance *Pempheris rhomboidea* (Figure 34A), *Pterois miles* (Figure 34B) and *Sargocentron rubrum*, in marine caves of this regions should be further studied and monitored (Gerovasileiou et al. 2016b, and unpublished data by both authors).

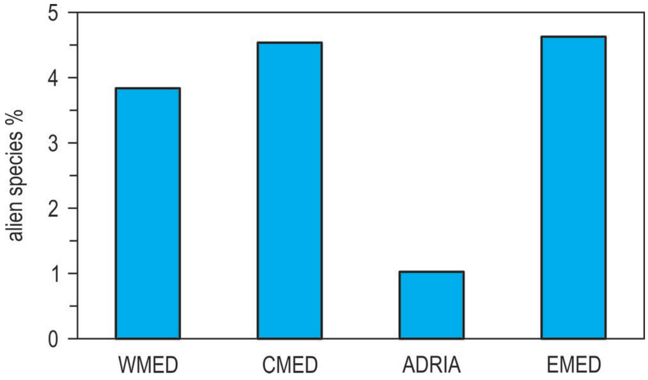

Figure 33 Occurrence of alien species in marine caves expressed as percentage of the total number of alien species known in the corresponding Mediterranean ecoregion. WMED: western Mediterranean: CMED: central Mediterranean; ADRIA: Adriatic Sea; EMED: eastern Mediterranean. Based on data from Gerovasileiou et al. (2016b).

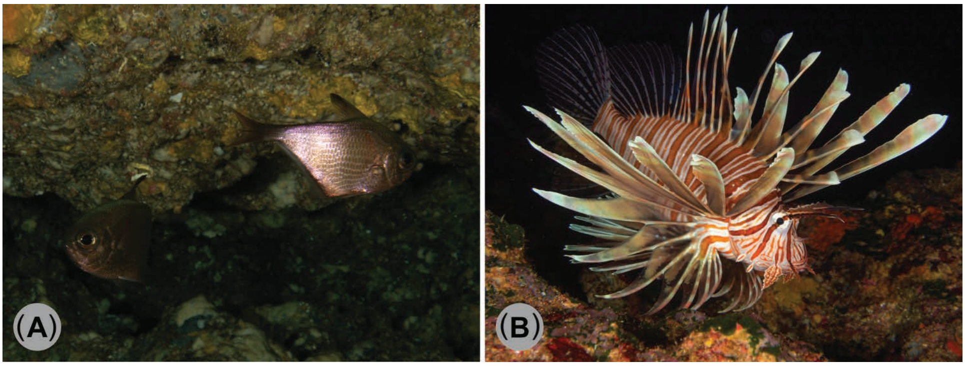

Figure 34 Several non-indigenous species of Indo-Pacific origin have invaded marine caves of the eastern Mediterranean Sea: (A) the sweeper *Pempheris rhomboidea* can form large schools in caves and crevices; (B) the highly invasive lion fish *Pterois miles* is common in marine caves of the Levantine, south Aegean and Ionian seas. Photos by T. Dailianis.

Conservation priorities and suggestions

Marine cave communities are characterized by high levels of 'individuality', generated by cave-specific topographical features (Bussotti et al. 2006, Gerovasileiou et al. 2013), 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). 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 microhabitats that could support unique communities (e.g. anchialine caves, marine caves with sulphur or internal freshwater springs, those having a descending profile or vertical pits, caves with bioconstructions)
- 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, Jimenez et al. 2019), it is important to safeguard good ecological status and maintain connectivity with nearby habitats (e.g. rocky reefs and *Posidonia* meadows) in conservation planning.

Gaps in scientific knowledge and future research directions

Despite the fact that marine caves of the Mediterranean Sea have been studied more intensively than those in any other region 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, several gaps and limitations came up, such as (1) lack of geographic coordinates and geomorphological information (e.g. water depth of the entrance and cave type) about numerous marine caves; (2) several caves having the same names (e.g. 'Blue Cave'); (3) lack of ecological information (e.g. cave zone and depth) about several taxa recorded from caves; and (4) 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. 2016a, 2020) 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 metadata). 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 regions.

Based on the gaps identified during the present and previous reviews, 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 regions, such as the north African, Aegean and Levantine coasts.
- Filling thematic gaps regarding particular groups of biota (e.g. microbial diversity and 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 or 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, human visitation).
- Investing in multidisciplinary, 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 (including monitoring) and restoration options/protocols, at different spatial scales in order to achieve future conservation targets.

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