

Fishes in Marine Caves

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Abstract: Fishes in marine caves have attracted limited attention by the scientific community in comparison to subterranean fishes which have lost eyes and pigmentation. They constitute a largely unexplored component of marine fish diversity, except for the relatively well-studied marine caves of the Mediterranean Sea. These habitats are characterized by steep environmental gradients of decreasing light and decreasing water exchange. The fishes recorded so far in marine caves are not exclusive residents of this habitat and they are also present at least in the other mesolithial habitats. In the Mediterranean marine caves, 132 fishes have been recorded to date, representing about 17% of the total Mediterranean fish species richness. Most of these species are reported from the anterior cave zones where some light still exists, while a smaller number of species are known from the totally dark zones. Among them, 27.3% are accidental visitors, 53.8% are the regular mesolithial visitors and switchers between mesolithion and open water, 5.3% are permanent residents of the mesolithion, but also occur in other habitats, and 13.6% are exclusive permanent residents of mesolithion. Some mesolithial exclusive permanent residents recorded in marine caves share similar morphology, probably as adaptations to these habitats.

Keywords: fishes; marine caves; mesolithion; ecology; adaptation; diversity; distribution



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Key Contribution: Marine caves are part of mesolithial habitats, together with pseudocaves and cryptobenthic habitats. Fishes recorded in marine caves are not exclusive cave residents. Five different morphological types of fish can be identified in relation to their adaptation to mesolithial habitats.

1. Introduction

The term “cave fish” is usually applied to “real” cave-exclusive species, also named subterranean or hypogean fishes [1]. As residents of subterranean habitats, these fishes are characterized as stygobitic species, considering that they inhabit aquatic subterranean environments [2] (Figure 1). Stygobitic and troglotic animals (i.e., the respective term for terrestrial animals) have evolved unusual and highly specialized morphological and life history traits for subterranean life (troglomorphy), being no longer able to survive above ground [3]. Troglotites and stygotites usually develop regressive features like the loss or reduction in size of the eyes and in pigmentation, but they also develop constructive traits, such as longer appendages and enhancements of nonvisual sensory systems [3]. Subterranean or hypogean fishes are restricted to underground freshwaters [4] and anchialine systems, with only fourteen species reported from anchialine systems in the last available summary [5].

Subterranean ecosystems include a variety of habitats ranging from aerobic caves and endolithic systems to underground streams and pools, groundwater ecosystems, anchialine systems and sea caves [6]. Marine caves (also known as sea caves) are globally distributed

in coastal headlands, rocky reefs and coral reefs [7] and constitute a characteristic feature of coastal areas with extensive rock outcrops such as the Mediterranean basin [8,9] (Figure 2).



Figure 1. *Garra longipinnis* cave form, Hotta Cave, Oman. Photo by H.R. Esmaili.

The study of the marine cave environment became possible only after the development of autonomous diving (SCUBA), which allowed not only marine cave exploration, but also direct observation and sampling by marine scientists [9]. The scientific study of marine caves started in the north Mediterranean Sea during the mid-twentieth century [10]. Marine caves are today acknowledged for their rich biodiversity [11]. The presence of fishes in marine caves was reported in the first exploratory surveys in these habitats [12,13]. Abel [12] published the first study on Mediterranean marine cave fishes. However, it soon became evident that marine caves do not host genuine stygobionts and that fishes, even if they are permanent residents of caves, show no adaptations similar to those of stygobitic species [13–15]. Proudlove [16], in his review of subterranean fishes, assigned sea cave fishes to the group of non-stygobitic fishes of caves and other subterranean habitats. Despite the existence of about seven decades of marine cave research, the fish fauna occurring in marine caves, including permanent residents, has been rarely investigated, with most available studies restricted to the Mediterranean Sea [17–19]. Therefore, this biotic component of the marine cave environment has never been extensively reviewed.

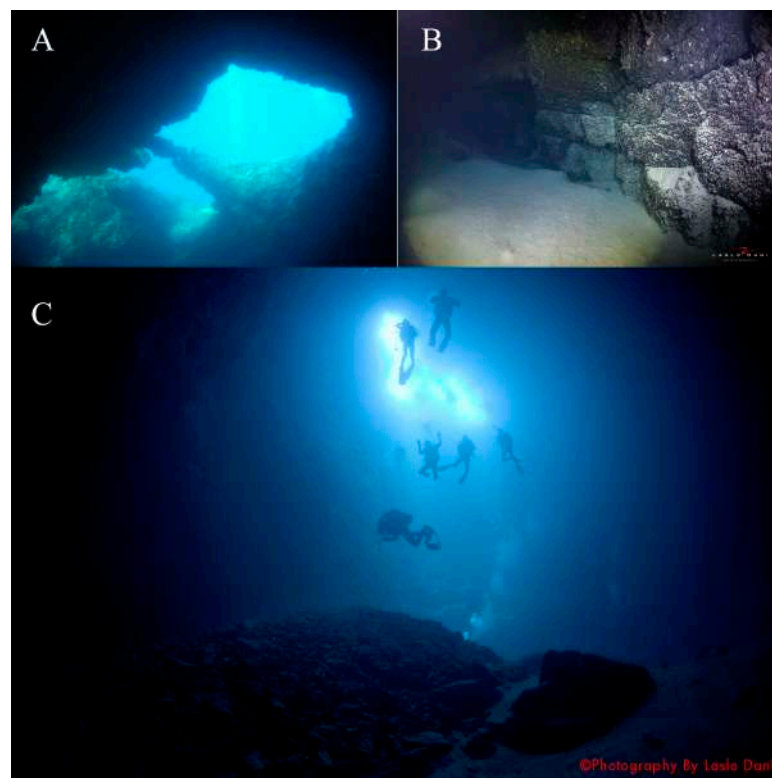


Figure 2. The marine cave Lučice, Adriatic Sea: (A) cave entrance, (B) and (C) interior. Photos by (A) M. Kovačić, (B) and (C) D. Laslo.

The aim of this work is to provide an overview of the existing knowledge on fishes in marine caves of the world and more specifically (a) to discuss their ecological relationships to caves; (b) to describe the biodiversity and distribution of fishes in marine caves and (c) to compare fish characteristics in marine caves with those known for other biota in aquatic subterranean ecosystems (freshwater and anchialine caves and open marine habitats). Ultimately, due to the limited available knowledge on the subject, this review highlights the main gaps of knowledge regarding fish fauna in marine caves and suggests future research directions. The applied taxonomy and nomenclature match that of Fricke et al. [20].

2. Marine Caves

The term “cave” is commonly applied to natural openings, usually in rocks, which are large enough for human entry [21,22]. This definition is clearly anthropocentric, implying also that a cavity is connected to the surface through entrances and can be distinguished from surface landforms by shape. Caves are geological formations whose long dimension (length or depth) is greater than the cross-sectional dimensions at the entrance [21]. Caves are formed by different processes in various rock types and in unconsolidated sediments. The great majority of natural caves, including the largest ones, are solution (or karst) caves, which have been created principally by the dissolution of bedrock (limestone and gypsum) by water circulating through initial openings such as fissures and pores [21]. Other caves, distinguished as to origin, are volcanic, glacier, crevice, littoral, pipe and erosion caves [21,23].

Marine caves are located either directly on the coast or can be wholly submerged beneath the sea floor and contain marine waters that freely exchange with the sea [23,24] (Figures 3 and 4). These caves are usually of littoral origin. Littoral caves, commonly known as sea caves, are found throughout the world, being formed either actively along present coastlines, or as relict sea caves on former coastlines [7,25]. The main driving force for the development of littoral caves is wave action. Erosion is ongoing wherever waves batter rocky coasts, but rock is removed at greater rates along sea cliffs which contain zones of weakness [25]. Flank margin caves are also formed at sea level but have a different origin [26]. They are formed by the corrosion at the mixing zone along the halocline in very young carbonates [8]. Blue holes constitute another kind of coastal cave, with several hypotheses about their formation [26]. Marine caves are not only formed at sea level but can also commonly form part of the submerged karst where original solution (or karst) continental caves were submerged due to a rise in sea level [8].

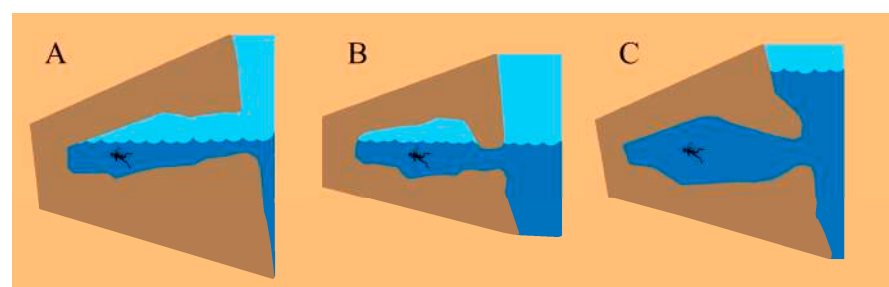


Figure 3. (A) Littoral or semi-submerged cave, (B) cave with internal air dome and (C) submerged blind-ended cave. Based on Riedl [13] and Gerovasileiou and Bianchi [9]. Drawing by M. Kovačić.

Anchialine caves differ from sea caves in terms of marine influence and connection to the atmosphere [27,28]. The influence of sea water in caves can extend beyond the coastline. Anchialine caves contain water bodies which have a subterranean connection to the sea and little or no direct connection to the atmosphere [28]. They can be found up to several kilometres inland from the coast and typically contain surface layers of freshwater or brackish water, separated by a thermochemocline from underlying fully marine waters, low in dissolved oxygen, which have a long residence time of months to years [24]. Therefore, the most striking abiotic ecological drivers of anchialine ecosystems are salinity gradients influenced by tides and currents, generating water stratification [28,29]. The main biological

characteristic of these habitats is the presence of a specialized anchialine fauna, consisting of stygobitic species of marine origin [28,29]. Anchialine caves usually occur in karstified limestone or in lava fields [29]. The delimitation of anchialine and marine environments in caves is not always clear. Blue holes can be found in the ocean or inland, with the former being open directly into the marine environment and usually containing marine water with tidal flow [30]. Inland blue holes are isolated by present topography from surface marine conditions and open directly onto the land surface or into an isolated pond or lake; they contain tidally influenced water with variable salinity, from fresh to marine [30]. Furthermore, some marine caves extend far enough inland so that water exchange is slow enough to resemble a true anchialine habitat [5]. Similarly, several inland anchialine systems have submerged entrances to the sea with significant influence by tides and currents, and thus the anterior part of these caves functions as a marine cave [5,28].

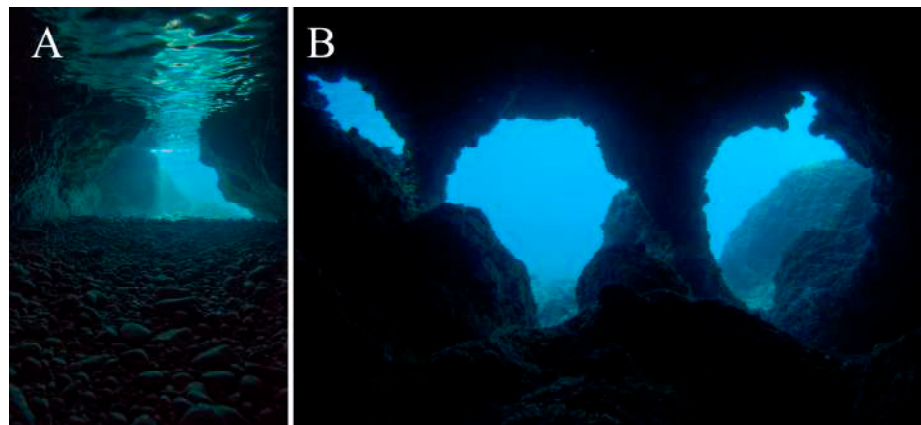


Figure 4. (A) Littoral or semi-submerged and (B) submerged cave entrance in Plave grote, Adriatic Sea. Photos by M. Babić.

Marine caves are present in the continental shelf of every continent. Despite their wide distribution in coastal headlands, rocky reefs and coral reefs of the world [7], studies on marine caves exist only for the well-studied seas. For example, in the Mediterranean Sea, while more than 3000 marine caves have been recorded so far, the actual number of marine caves is expected to be much higher [9]. Most of the studied caves are usually semi-submerged, or shallow marine caves with a maximum depth of their entrances not exceeding 15 m. Only a small number of the studied marine caves in the Mediterranean Sea are located at a depth range of 15–40 m, and no caves have been studied for their biota below this depth [9,11]. The restricted depth range of the studied marine caves is caused by the limits of employed methods (usually SCUBA diving) as well as the shallow bathymetric distribution of most of the known marine caves. However, it could be expected that marine caves are present in the entire range of earlier variation of the coastline, down to the present seabed depth of 135 m, considering that the last glacial maximum occurred 26 thousand years ago [8]. Deep marine caves inhabited by coelacanths *Latimeria chalumnae* Smith, 1939 were discovered in submarine canyons in South Africa, at a depth range of 96–133 m, by using a research submersible [31]. Marine caves inhabited by coelacanths and other fishes have also been found in deeper waters, down to 250 m in Comoros [32,33]. These are probably the deepest records of fishes in marine caves known to date. Furthermore, recent surveys in the deep Mediterranean Sea with Remotely Operated Vehicles (ROVs) have shown that hard substrata in deeper waters can also have cave formations below the continental shelf, in the upper bathyal zone at depths down to 795 m, possibly dating back to the Messinian salinity crisis, 5.96–5.33 million years ago [34,35].

Another difference between most marine caves and anchialine or freshwater caves which affects the synthesis and distribution of their biota concerns their dimensions. Many continental caves, including those with freshwater or anchialine systems, are longer than

100 km [36], while the longest known marine cave is Matainaka Cave on New Zealand's South Island with a total length of 1.54 km [37]. Most studied marine caves do not exceed 100 m in length, and the average size of most studied marine caves is usually measured in tens of metres [25].

Considering smaller cryptic environments at the rocky bed (e.g., cavities, rock crevices and fissures), which may have a wide range of shapes and sizes, the anthropocentric definition of caves excludes them from the marine caves *sensu stricto*. The evolution of the definition of marine caves can be followed from Riedl [13] to Gerovasileiou and Bianchi [9]. The latter authors performed an extensive review of available knowledge and 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 with a possible quantitative criterion that the ratio between the numbers expressing the total volume (in m³) and the entrance area (in m²) must be greater than 1, and that the width of the entry must not exceed the internal average" (Figure 5A–D). This excludes semi-closed "pseudocaves", specifically larger crevices, gaps, overhanging rocks and coral formations [38] (Figure 5E,F). Marine cave walls and ceilings consist of hard substrate, while the substrate of the cave floor can be either soft or hard [15]. With regard to submersion level and morphology, marine caves can be either submerged or semi-submerged, blind-ended (or cul-de-sac) (Figure 5A,B,E) or with multiple openings (tunnels) [9,13] (Figure 5C,D,F). In addition, holes or crevices within sea caves form caves within caves [15].

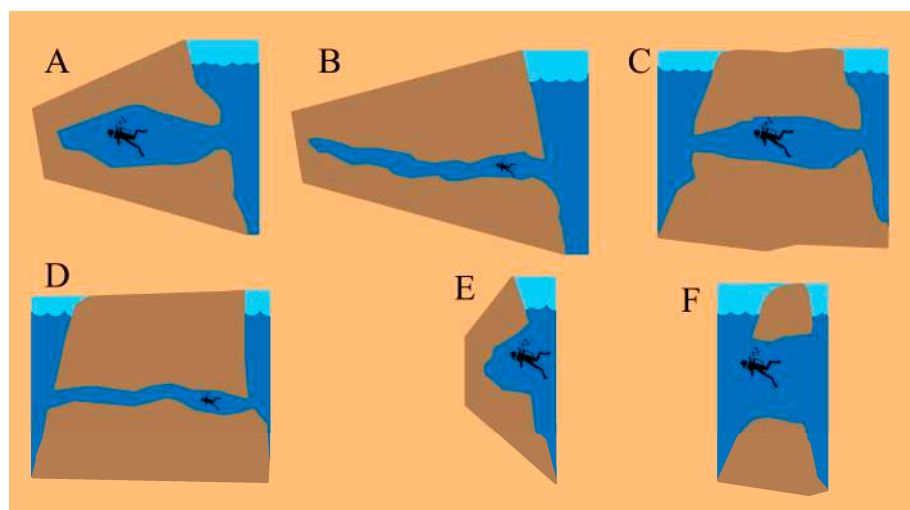


Figure 5. Submersed caves (A–D) *sensu* Gerovasileiou and Bianchi [9] and pseudocaves (E,F) *sensu* Zander [38] of blind-ended (A,B,E) and tunnel-shaped morphology (C,D,F). Based on Riedl [13] and Gerovasileiou and Bianchi [9]. Drawing by M. Kovačić.

The main abiotic parameters influencing the composition of biota inside marine caves are decreasing light, decreasing hydrodynamism and substrate type [9,13]. Environmental gradients such as the decrease in light, water movement and trophic input inside marine caves are intense, occurring within a few metres. The same decrease in the external open benthic environment can take place within tens or even hundreds of metres [9]. These gradients influence species distributions inside marine caves and generate a marked zonation of cave communities [9]. Cave entrances are usually dominated by sciaphilic macroalgae and benthic invertebrates, while the inner semidark and dark cave biocoenoses are animal-dominated. The dark interior of marine caves is generally characterized by a much lower biotic cover, species richness, biomass and three-dimensional complexity compared to the anterior cave zones [9]. Light conditions, water exchange and biotic features inside caves largely depend on the specific cave topography such as dimensions of the entrance, shape and length of the cave. For example, many short sea caves may completely lack an inner dark zone but still fit the cave definition [9,13].

3. Fishes in Marine Caves

3.1. History of Research and Knowledge on Fishes in Marine Caves

The study of fishes in marine caves, *sensu* Gerovasileiou and Bianchi [9], started in the second half of the twentieth century in the Mediterranean Sea and has remained mostly geographically restricted to this sea, with the published data still being scarce and limited elsewhere. Available data about fishes in marine caves are also restricted to those caves occurring in the upper littoral or infralittoral zone (i.e., the bathymetric zone from the lower limit of the tidal range down to the lowest limit where photophilic algae can live). The pioneering study by Laborel and Vacelet [39] in the Niolon cave of France mentioned two fish species, *Apogon imberbis* (Linnaeus, 1758) (Figure 6A) and *Serranus cabrilla* (Linnaeus, 1758).



Figure 6. (A) *Apogon imberbis* (Linnaeus, 1758); (B) *Chlidichthys auratus* Lubbock, 1975; (C) *Anthias anthias* (Linnaeus, 1758); (D) *Sargocentron rubrum* (Forsskål, 1775); (E) *Myripristis kuntee* Valenciennes, 1831; (F) *Priacanthus blochii* Bleeker, 1853. Photo (A,C,D): R.A. Patzner; (B): S.V. Bogorodsky; (E,F): K. Hagiwara.

Abel [12] published the first detailed study about marine cave fishes from a marine cave in the Gulf of Naples (Italy), recording 32 species, and divided fishes, according to their relationship to caves, into speleoxenous, speleophilous and speleobiont species. He also divided caves, from the animal point of view, into the larger marine caves or “optical caves” and the small hidden spaces of “thigmotaxic caves”. The next important step in the study of marine caves was Riedl’s [13] influential monograph on the ecology of marine caves, *Biologie der Meereshöhlen*, which summarized records of 43 fish species from Mediterranean marine caves and included the first record of an alien species in a marine cave habitat, *Sargocentron rubrum* (Forsskål, 1775) from Lebanon (Figure 6D). However, the definition of marine caves in Riedl [13] also included other cryptic habitats at the seabed. During the 1960s, records of fishes in marine caves were rare, e.g., [40,41]. After these pioneering

studies, Bath [42] described a new fish genus and species from a Mediterranean marine cave, the goby *Gammogobius steinitzi* Bath, 1971 (Figure 7C). Zander and Jelinek [43] studied fish fauna in the Banjole cave, in the Adriatic Sea, and its relationship to light availability within this cave. They also described both a new genus and species of gobies, *Speleogobius trigloides* Zander & Jelinek, 1976 from the Banjole cave (Figure 7A,B). The second alien fish record in a Mediterranean marine cave, *Pempheris rhomboidea* Kossmann & Räuber, 1877 (Figure 7D) (as *Pempheris vanicolensis* Cuvier & Valenciennes, 1831), was recorded in 1979 in Lebanon [44]. The first studies on the ecology of individual fish species in marine caves also started in the 1970s [45,46].

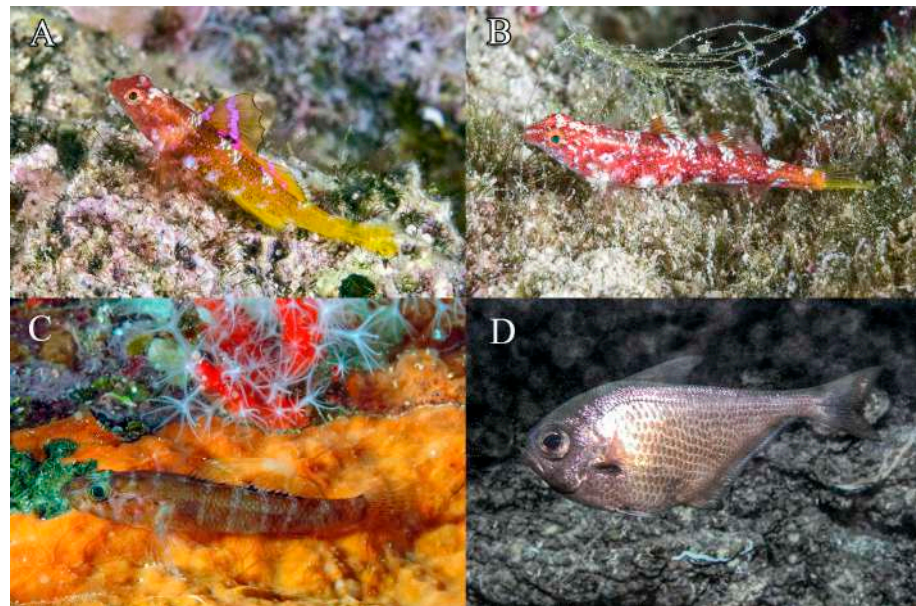


Figure 7. (A) *Speleogobius trigloides* Zander & Jelinek, 1976, male; (B) *S. trigloides* female; (C) *Gammogobius steinitzi* Bath, 1971; (D) *Pempheris rhomboidea*. Photo (A,B): R. Svensen; (C): S. Guerrieri; (D): R.A. Patzner.

During the 1980s only a few studies about marine caves included information about fish species, e.g., [47–50]. The first paper dedicated to the fish assemblages in marine caves, following Abel [12] and Zander and Jelinek [43], was published by Zander [14]. He studied fishes from the Mediterranean marine caves and associated habitats, applying the term “mesolithial habitats” for all cave-like habitats independently of their size (i.e., including marine caves, overhangs as well as crevice microhabitats). At the end of the twentieth century, several papers described [51–53] or extended [54–59] the known geographic distribution of Mediterranean fishes in marine caves. Some studies dealing with cryptobenthic fishes also reported species from marine caves among other cryptic habitats [60,61]. Arko-Pijevac et al. [62] studied the biocoenoses of a submarine cave on the island of Krk (Croatia, Adriatic Sea), and among more than one hundred animal species, they also recorded 20 fish species. Bussotti et al. [63] performed the first quantitative research of fish assemblages in marine caves, using the visual census method, and recorded 19 fish species in shallow marine caves of the Salento Peninsula (Apulia, Italy). Bussotti et al. [64] showed, in another quantitative study, that marine caves are the preferred habitats of the cardinal fish *A. imberbis*. Harmelin et al. [65] studied a small, submerged cave in Bagaud Island (Port-Cros National Park, France) and recorded 19 species, including 11 cave-dwellers and eight occasional visitors. Belmonte et al. [66] studied the marine caves of Albania for the first time and recorded six fish species. The most distant record of marine fish inside a marine cave was that of *Chelon* sp. (reported as *Liza* sp.), found more than 1000 m away from the cave entrance in the cave system of the Grotta del Bel Torrente in Sardinia, Italy [67]. In addition to *Chelon* sp., the species *Conger conger* (Linnaeus, 1758) and *Solea solea* (Linnaeus, 1758) were recorded at 500 and 340 m from the entrance

of the same cave, respectively. In another quantitative study, Bussotti and Guidetti [68] studied dissimilarities of fish assemblages between marine caves and rocky cliffs in Salento Peninsula (Apulia, Italy), with 29 fish species recorded inside cave habitats and 10 of them observed exclusively inside caves. Bussotti and Guidetti [69] similarly recorded 37 fish species inside cave habitats.

During the last decade, research on Mediterranean marine cave fishes has intensified, providing data from previously under-studied marine areas along with quantitative data on fish abundance and habitat preferences. Bussotti et al. [17] used visual census to study fish fauna in 14 marine caves of Italian marine protected areas and recorded 38 species. Later, Bussotti et al. [70] studied 16 marine caves along the coasts of Spain, France and Italy with visual census and recorded 33 fish species while also highlighting the potential role of *A. imberbis* (Figure 6A) for cave ecosystem functioning in the western Mediterranean. In the eastern Mediterranean, Gerovasileiou et al. [71] combined new data from marine caves of the Aegean Sea with literature data from the entire eastern Mediterranean basin and reported 37 fish species. New data on fishes in marine caves were also published from Croatia [72], Greece [19,73], Italy [74], Cyprus [75], Montenegro [76], Turkey [77–79], Israel [80] and Malta [35]. Most of the above-mentioned studies provided information about fishes as part of general ecological and biodiversity cave assessments, while two studies focused specifically on rarely reported cryptobenthic fishes [19,73], and one study focused on fishes in six caves of the Aegean coasts of Turkey recording 32 species [77]. More recently, Kovačić et al. [18] studied “cave within cave” fishes in a marine cave of Croatia using the methods for cryptobenthic fishes (Figure 8), recording 18 species inside the marine caves. Fifteen of these species were sampled by using the square and anaesthetic method, with nine species found in intracave cavities, including five species which occurred exclusively in this “cave within cave” highly cryptic habitat. The last available census reported a total of 112 fish species from Mediterranean marine caves [9]. Among these, 18 species are introduced, mainly originating from the Indo-Pacific Ocean [81,82].

The lack of studies on fishes in marine caves *sensu stricto* and their geographic limit to the Mediterranean Sea was also emphasized by the short review on fishes in sea caves in Proudlove’s [1] capital work on subterranean fishes. To the best of our knowledge, published records of fishes from marine caves *sensu stricto* outside the Mediterranean Sea, excluding anchialine systems, are limited from all other areas, e.g., the Pacific Ocean, specifically Sulawesi Island [83], Japan [84–86], Hong Kong [87], Hawaiian Islands [88], Palau [89], Australia [90–92], Vietnam [93], Indonesia [94] and Micronesia [86]; the Red Sea and Indian Ocean, specifically the northwest Indian Ocean and the Red Sea [38,95,96], Comoros Islands [32,33] and South Africa [31]; and the Atlantic Ocean, specifically Azores [97]; Bermuda [98] and the Black Sea [99,100].

The studies of fishes in marine caves *sensu stricto* outside the Mediterranean Sea are mostly restricted to taxonomy, including new species descriptions from marine caves (Apogonidae: [94]; Bythitidae: [83,84,88,101]; Gobiidae: [85,92,96]; Protoanguilidae: [89] (Figure 9A); Pseudochromidae: [95] (Figure 6B); Serranidae, Anthiinae: [86,91]), as well as new records of fish species [99] and studies on a single species [31,32]. Species of the genus *Lucifuga* Poey, 1858 were also recorded from marine blue holes, even though euryhaline species of this genus are regularly found in inland caves and anchialine systems [101]. Some species in marine caves were recognized as new but still remain undescribed [102]. Only a few studies specifically focus on fishes recorded within a targeted fish census in marine caves [87,98] or report on the fish fauna as the part of the cave biota in ecological and biodiversity assessments [90,93,97,100,103]. Depczynski and Bellwood [104] studied cryptobenthic reef fish communities in Australia in four distinct microhabitats, including marine caves. They recorded 26 cryptobenthic fish species in marine caves, mostly Gobiidae and Apogonidae, but also species of several other fish families, with four species exclusively found in marine caves. However, their definition of marine caves also included pseudocaves, and it is not clear if any marine caves *sensu stricto* were actually studied. The study of Zander [38] on the Red Sea coast of Egypt also covered fishes from pseudocaves

and not marine caves *sensu stricto*. Fishes have been also recorded in deep-water caves at the continental shelf break and below in the Southwestern Indian Ocean [31–33].

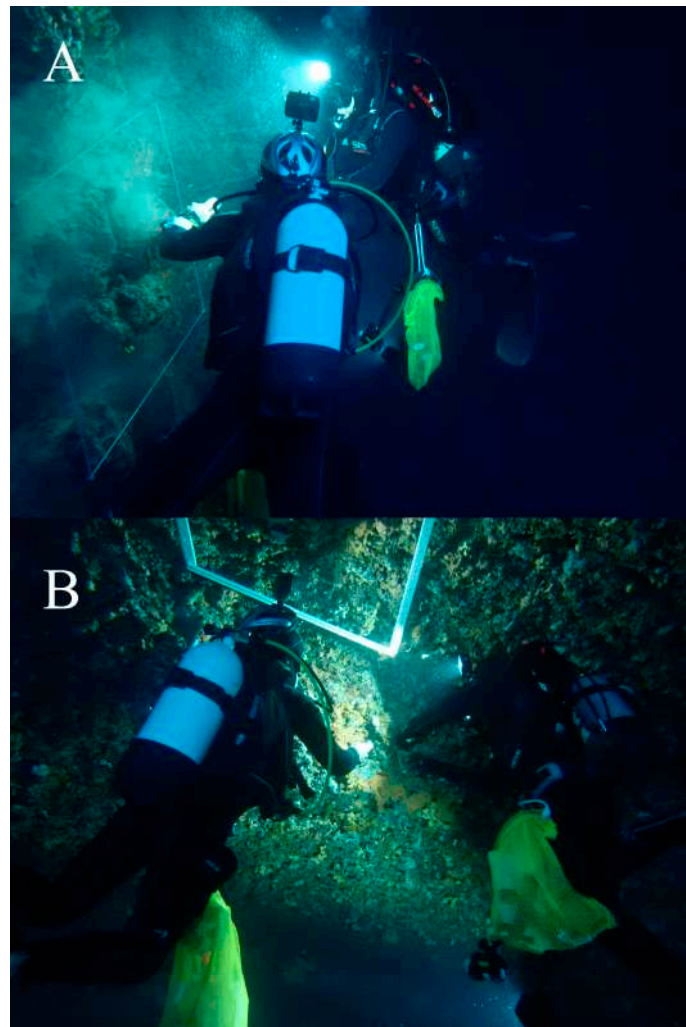


Figure 8. Square collecting of cryptobenthic fish on (A) the wall and (B) the ceiling in the marine cave. Photos by Z. Valić.

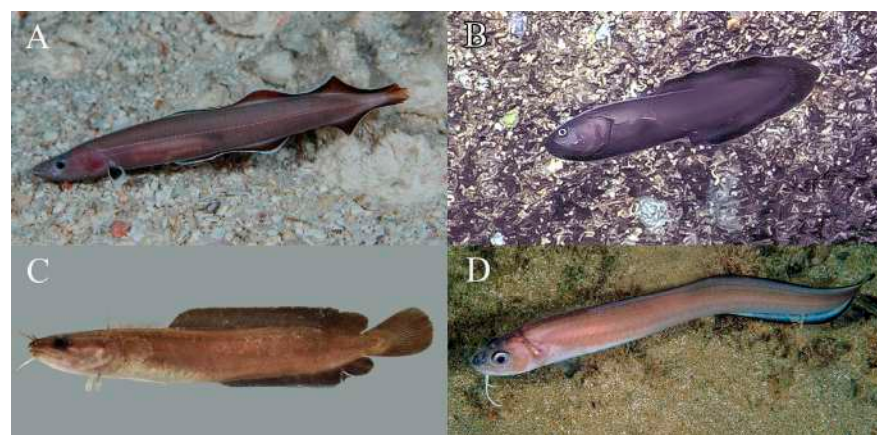


Figure 9. (A) *Protanguilla palau* Johnson, Ida & Sakaue 2012, new species, genus and family described from marine cave, photo by J. Sakue. (B) *Grammonus ater* (Risso, 1810), photo by R.A. Patzner. (C) *Gaidropsarus mediterraneus* (Linnaeus, 1758), photo by M. Kovačić. (D) *Ophidion barbatum*, photo by S. Guerrieri.

3.2. Fishes in Marine Caves as a Part of Mesolithial Habitats

3.2.1. Ecological Classifications of Fishes in Marine Caves

The Schiner–Racovitza system [105,106] divides subterranean diversity into troglobites, troglaphiles and troglaxenes. Trajano [106] redefined the Schiner–Racovitza categories: troglobites or troglabionts correspond to exclusive subterranean source populations; sink populations may be found in surface habitats; troglaphiles include source populations both in hypogean and epigean habitats, with individuals regularly commuting between these habitats, promoting the introgression of genes selected under epigean regimes into subterranean populations (and vice-versa); troglaxenes are instances of source populations in epigean habitats, but using subterranean resources (the so-called obligatory troglaxenes are dependent on both surface and subterranean resources).

Abel [12] divided fishes in marine caves according to their relationship with caves to speleoxenous, speleophilous and speleobiont species, a division superficially similar to the Schiner–Racovitza system. According to Abel [12], the cave-avoiding species (speleoxenous fish) are opposed to obligate cave settlers (speleobionts), while the fishes occasionally found in cave systems (speleophilous fishes) can be further divided into those that temporarily visit caves as shelters and those that occasionally colonize caves. However, Riedl [13], who studied the entire invertebrate fauna in addition to fishes in marine caves, concluded that the inhabitants of marine caves are not an independent fauna, but speleophilic forms whose populations are connected via the open sea, and classified fishes only into speleophilic, indifferent and speleophobic fishes. Indeed, no genuine speleobiontic fishes have been found to date in marine caves, and permanent cave-dwellers do not show any adaptation similar to those found in the stygobitic fishes [13–16]. For example, the three fish species originally designated as obligate cave settlers by Abel [12], *Anthias anthias* (Linnaeus, 1758) (Figure 6C), *Microlipophrys nigriceps* (Vinciguerra, 1883) (Figure 10A,C) and *Tripterygion minor* Kolombatović, 1892 (Figure 10B), can also be found in other marine benthic habitats with dim light and decreasing currents [107]. Zander [14] noticed that the same fish species, that he designated as speleophilic, occurred in different habitats such as marine caves (*sensu* Gerovasileiou and Bianchi [9]), shaded spaces below overhangs or in the crevicular microhabitats. Therefore, he proposed the term “mesolithion” (meaning between stones) for this community, deriving from the Greek words “meso” (μέσο), meaning “middle” or “between”, and “lithos” (λίθος), which means “stone” or “rock”. Zander also distinguished speleophilous fish, which are photophobic or heliophobic versus euryphotic fishes [14,15,43]. He also gave examples of the ecological classification of fishes in marine caves of the Red Sea, specifically speleoxenous fish, like *Pseudanthias squamipinnis* (Peters, 1885), which may be found in cavities and also in open water, while speleophilous fish use the cave as a resting or hiding place as with most day active species (e.g., *Pseudochromis fridmani* Klausewitz, 1968, serranids or chaetodontids). As Zander’s [38] study was performed in pseudocaves, his use of Abel’s *speleo*-terms is not really suitable for pseudocaves and for the mesolithion as a whole. In addition to the absence of genuine speleobionts restricted to marine caves, the existence of the exclusive permanent fish residents of the mesolithial habitats in general should be clarified and described more fully.

Apart from the Mediterranean Sea, there exist very few examples of the classification of fishes according to their relationship with marine caves. For instance, Micael et al. [97] distinguished residents, seasonal and occasional species among eleven fish species recorded in a subtidal tunnel of São Miguel Island in Azores, Atlantic Ocean.

Understanding the position of benthic fishes in relation to the bottom is also necessary for studying and explaining the habits of mesolithial fishes (Figure 11). Cryptobenthic fish live in the small hidden spaces underneath the bottom surface; epibenthic fish lie on the bottom surface with physical contact with the substrate; hyperbenthic fish swim or hover above the bottom, more or less within 1 m from the surface [108,109] (Figure 11). The position to the bottom is characteristic of any individual in a particular moment, but it can be generalized for species when they exclusively or predominantly occur in one position or

microhabitat [109]. The relationship of benthic fish species with the bottom influences their body form [110], so that the latter can be indicative of where and how the fish species lives.



Figure 10. (A) *Microlipophrys nigriceps* (Vinciguerra, 1883) (Blenniidae, northern Mediterranean); (B) *Tripterygion minor* Kolombatović, 1892 (Tripterygiidae, northern Med.); (C) *M. nigriceps* (southern Med.); (D) *Tripterygion melanurus* Guichenot, 1850 (southern Med.). Photo (A,C,D): R.A. Patzner; (B): M. Kovačić.

Benthopelagic fishes, like *Boops boops* (Linnaeus, 1758), and neritic epipelagic fishes, like *Seriola dumerili* (Risso, 1810), have also been recorded from the water column inside large marine caves [71], though clearly as accidental visitors. In common with benthic categories, categorization of these fishes by pelagic zones should also be defined in the assignment of species recorded in marine caves to different pelagic zones: littoral benthopelagic fishes live and feed near the seabed, as well as in midwaters or near the surface [111]; epipelagic fishes live and feed in the open sea in the surface waters or at midwater to depths of 200 m, while neritic fishes live in the shallow pelagic zone over the continental shelf in nearshore marine ecosystems [111] (Figure 11).

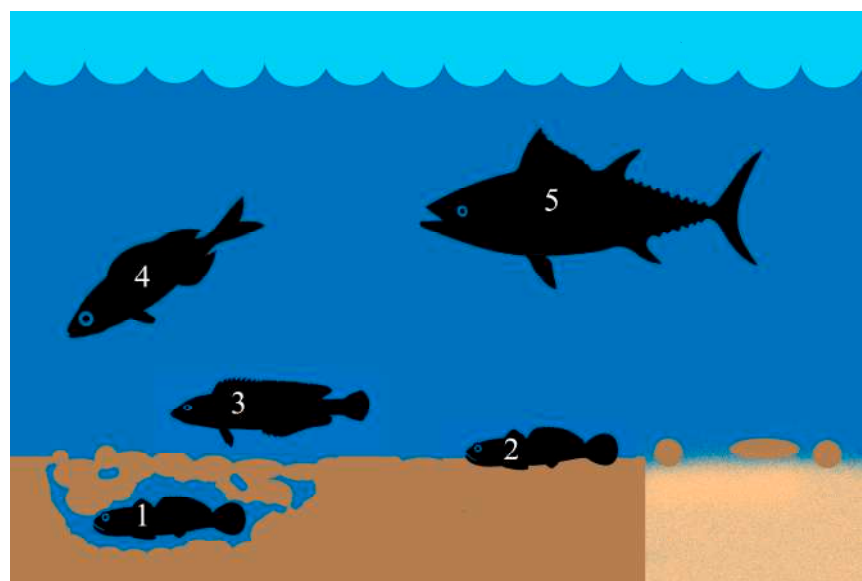


Figure 11. Habitat position of fishes occurring in marine caves. Benthic fishes: (1) cryptobenthic fish, (2) epibenthic fish, (3) hyperbenthic fish. Pelagic fishes: (4) benthopelagic fishes, (5) neritic epipelagic fishes. Drawing by M. Kovačić.

3.2.2. Mesolithial Fish

Marine caves *sensu stricto* apparently lack independent fish fauna and genuine speleobiontic fishes, since marine caves share fish fauna at least with the other mesolithial habitats [13–15]. The terms accidental cave visitors, regular cave visitors, switchers between caves and open water, and finally, cave permanent residents (including both those that occur in other habitats and those which are cave exclusive permanent residents) should be, therefore, expanded to the entire mesolithion [14] (Table 1). Abel’s [12] classification of accidental cave visitors, occasional cave dwellers and cave-exclusive dwellers, with a number of subcategories, corresponds to the categories used in the present classification (Table 1).

Table 1. Classification of fish presence in the mesolithial habitats and Abel’s (1959) corresponding categories.

Fish Presence in Mesolithion	Abel’s [12] Corresponding Categories
1. Accidental visitors	A, B.I.a
2. Regular visitors and switchers between mesolithion and open water:	
2.1. Visitors and switchers with no time regularity	B.I.b, B.I.c, B.III.a in part, B.III.b in part
2.2. Diel switchers	B.II.b, B.II.c
2.3. Seasonal switchers	B.II.a
3. Permanent residents whose populations also occur in other habitats but individuals do not migrate	B.III.a in part, B.III.b in part
4. Exclusive permanent residents	C

The terms “mesolithion” community and its “mesolithial” habitats are defined as the parts of the littoral system with dim light and decreasing currents, where sedentary suspension feeders dominate [14,15]. The term mesolithial habitats is applied to marine caves in a broad sense [13]. According to Zander [38], caves, pseudocaves and cryptobenthic habitats are specific habitats of the mesolithion (Figure 12). Therefore, mesolithial habitats include: (1) “cryptobenthic” habitats, specifically the small restricted living spaces underneath the surface of the seabed’s substrate or biocover, with a physical barrier to any open spaces (e.g., cavities, crevices in bedrock, interstitial spaces among boulders, pebbles or gravels, or spaces produced by biocover), which harbour “cryptobenthos” such as small-sized cryptobenthic fishes [109]; (2) “pseudocaves”, specifically larger crevices, gaps, overhanging rocks and coral formations, where the greatest proportion of fish is hyperbenthic [38], though epibenthic and cryptobenthic fishes may also be present; and (3) “real” marine caves, having large, mostly closed spaces where light and currents decrease sharply [14,38] (Figure 12). Marine caves are inhabited by hyperbenthic and epibenthic fishes [38], as well as by cryptobenthic fishes present in “cave within cave” small spaces inside marine caves [18] (Figure 12). The term “mostly closed” means that the marine cave opening to the outer environment is small compared to total surface area of the cave (in contrast to pseudocaves), while the term “large size” means that marine caves have enough space to contain large motile fauna such as hyperbenthic fishes, which cryptobenthic habitats do not usually have. Abel’s [12] term for “thigmotaxic caves” actually refers to “cryptobenthic” habitats, which occur as crevices, holes and cavities on the sea floor, but also as “cave within cave” inside larger “optical caves” [12]. The described characteristics of the third listed type of mesolithial habitats, “real” marine caves, correspond more or less to the definition of marine caves *sensu* Gerovasileiou and Bianchi [9] (Figure 12).

The two examples provided by Zander [38] for the ecological classification of fish species in the Red Sea pseudocaves (*Pseudanthias squamipinnis* and *Pseudochromis fridmani*) correspond to a mesolithial visitor and to a diel switcher between the mesolithion and the open water, respectively (Table 1). Therefore, none of these exemplifies the permanent mesolithial residents. On the other hand, the three examples of “speleobiont” fishes by Abel [12], *A. anthias* (Figure 6C), *M. nigriceps* (Figure 10A,C), and *T. minor* (Figure 10D), can be confirmed as exclusive permanent mesolithial residents, rarely or never seen outside these habitats (Table 1). Nevertheless, it remains unclear as to whether the dependence of

A. anthias on hidden habitats continues to the deep benthic environments of circalittoral rocky beds [107].



Figure 12. Mesolithial habitats. (A) Marine caves *sensu* Gerovasileiou and Bianchi [9]. (B) Pseudocaves *sensu* Zander [38]. (C) “Cryptobenthic” habitats *sensu* Kovačić et al. [109]. Drawing by M. Kovačić.

3.2.3. Permanent Mesolithial Residents in Marine Caves

Permanent mesolithial residents includes cryptobenthic fishes as well as hyperbenthic and epibenthic fishes using larger volumes of caves and pseudocaves [18,19,38].

Cryptobenthic fishes are well-studied in the Mediterranean Sea (Glavičić et al. [112] and references therein), with the data also available for marine caves [18,19]. Available quantitative studies have found that the gobies *Odondebuena balearica* (Pellegrin & Fage, 1907), *Zebrus zebrus* (Risso, 1827) (Figure 13A) and *Corcyrogobius liechtensteini* (Kolombatović, 1891) (Figure 13B), are among the most frequent and abundant cryptobenthic fishes of the littoral zone of the Adriatic Sea (Glavičić et al. [112] and references therein) (Figure 13). In addition to Gobiidae, other cryptobenthic permanent mesolithial residents of the Mediterranean Sea belong to the families Blenniidae, Gobiesocidae and Tripterygiidae (Glavičić et al. [112] and references therein). These small fishes are not merely permanent mesolithial residents but are also exclusive mesolithial residents which do not inhabit other habitats and are rarely recorded outside cryptic habitats (Glavičić et al. [112] and references therein). In the “cave within cave” microhabitat of Mediterranean marine caves *sensu stricto*, the dominant fish species composition of cryptobenthic fishes is slightly different, with *C. liechtensteini* (Figure 13B), *Marcelogobius splechnai* (Ahnelt & Patzner, 1995) (Figure 13D) and *Z. zebrus* (Figure 13A) prevailing in terms of abundance and frequency of occurrence over other cave fish species [18] (Figure 12). Again, all these species belong to the family Gobiidae. Due to the limited size and mobility of these species it might be expected that the individuals found inside caves are, after settling of larvae, the lifetime cave residents, although these species can be also found in other mesolithial habitats as well. *Gammogobius steintzi* Bath, 1971 (Figure 7C) is the only species among gobies in marine caves with published records known only from marine caves *sensu stricto* [99]. However, this species is not an exclusive cave resident, as it has been observed outside caves in other mesolithial habitats by one of the authors (MK) in the north and middle Adriatic Sea (samples were collected and stored in the collection of the Natural History Museum Rijeka, Croatia).

Studies about marine cave fauna often completely miss not only the cryptobenthic fish fauna of inner cave parts, but also the cryptobenthic fish fauna of shallow caves and cave entrances which are characterized by more light. For example, Gerovasileiou et al. [71] listed 37 fish species from 66 marine caves of the eastern Mediterranean Sea based on targeted cave surveys, information provided by recreational divers, and the published scientific literature, and yet they only recorded one cryptobenthic fish, the gobiesocid *Lepadogaster candolii* Risso, 1810. Specifically, this species was found inside the canals of the sponge *Aplysina aerophoba* (Nardo, 1833) in the semidark part of a large and deep Aegean cave [71]. The attention paid to cryptobenthic fish of Mediterranean marine

caves has recently benefited by the works of Ragkousis et al. [19] in the Aegean Sea and Kovačić et al. [18] in the Adriatic Sea. These works increased the knowledge on the diversity, abundance, distribution and ecology of cryptobenthic and other small fishes of marine caves in the Mediterranean Sea, recording nine species and 15 species, respectively.



Figure 13. (A) *Zebrus zebrus* (Risso, 1827); (B) *Corcyrogobius liechtensteini* (Kolombatović, 1891); (C) *Lepadogaster lepadogaster* (Bonnaterre, 1788); (D) *Marcelogobius splechnai* (Ahnelt & Patzner, 1995). Photo (A,C): R.A. Patzner; (B,D): S. Le Bris.

Fish adaptations to small, flat or narrow spaces of the cryptobenthic component of mesolithion include size reduction and changes in shape, mostly in gobies and clingfishes [113,114]. The shape adaptation found by Vukić et al. [114], consists of reduced body size with large head and large jaw width to body size ratio, stout anterior part of the body, and robust body. These adaptations make these fish large predators with small bodies inside the small spaces, such as the Mediterranean gobiid *Z. zebrus* (Figure 13A) or the clingfish *Lepadogaster lepadogaster* (Bonnaterre, 1788) (Figure 13B), both also recorded in marine caves. Another kind of cryptobenthic adaptation includes a small, elongated body with flattened head, more suited for moving inside interstitial spaces of multiple layers of particles, such as in the Mediterranean genus *Chromogobius* de Buen, 1930 (Figure 14A). Extreme adaptations of this type are found in fish inhabiting the interstitium of gravel beaches, such as the Western Pacific gobiid genus *Luciogobius* Gill, 1859 and the Mediterranean clingfish genus *Gouania* Nardo, 1833 (Figure 14B). In addition to the elongated body with flattened head, gravel-inhabiting *Gouania* species show adaptation with troglomorphic elements, specifically reduced pigmentation and small eyes, although both are still present [16,113]. The species of both genera, *Chromogobius* and *Gouania*, were also recorded in marine caves (Table 2). All these fishes are permanent and exclusive mesolithial residents, which do not inhabit other habitats and are never or rarely recorded outside cryptic habitats.

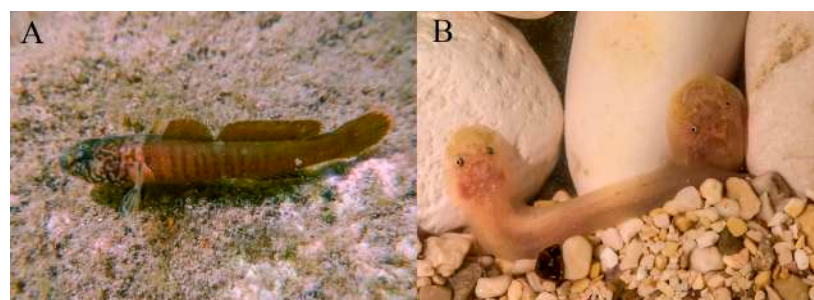


Figure 14. (A) *Chromogobius quadrivittatus* (Steindachner, 1863); (B) *Gouania pigra* (Nardo, 1827). Photo (A): M. Kovačić; (B): M. Wagner.

Small fishes that are permanent and exclusive residents of dimly sheltered mesolithial habitats are not necessarily permanently utilizing “cave within cave” microhabitats. Some species occur regularly on open inner surfaces of caves and pseudocaves, such as the Mediterranean *Tripterygion melanurus* Guichenot, 1850 (Figure 10D), *T. minor* (Figure 10B) and *M. nigriceps* (Figure 10A,C) (Table 2) [45,46]. At the microhabitat scale, they function as the epibenthic fish within larger cryptic spaces, looking for shelters or “thigmotaxic caves” *sensu* Abel [12], only when scared or chased. However, Abel [12] distinguished *M. nigriceps* and *T. minor*, observing that *M. nigriceps* still has regular hiding places within the cave, while *T. minor* does not. The “epibenthic” position means lying on the inner cave surface, which also includes the attached position to vertical walls or the upside-down position on the roof of the larger space. Neither of these three species has any types of morphological adaptation such as those described for cryptobenthic permanent mesolithial residents. They are just small, with slender bodies and a colouration pattern dominated by mostly and more or less uniformly red or orange colour, which looks like the third body type adaptation to mesolithion, in addition to two cryptobenthic body shapes. Two large genera of Indo-Pacific gobies with about a hundred different species, *Eviota* Jenkins, 1903 and *Trimma* Jordan & Seale, 1906, include numerous small species described from habitats matching with the definition of mesolithial habitats and some of them even in the marine caves *sensu stricto* [85,92,96]. Hagiwara and Winterbottom [85] stated that *Trimma hayashii* Hagiwara & Winterbottom, 2007 often stays in an “epibenthic” upside-down position on the ceiling of the larger space, like the Mediterranean fish described before, but *Trimma flavatrum* Hagiwara & Winterbottom, 2007 (Figure 15A) forms small schools hovering close to the surface in caves, always with the ventral side facing the nearest substrate, so when schools are close to ceilings, it resembles strange upside-down hovering and hyperbenthic behaviour. The hovering near the cave roof behaviour was also observed in the Red Sea *Trimma nubarum* Winterbottom, Bogorodsky & Alpermann, 2023 (Figure 15B) [96]. Many *Trimma* species live or can be found in caves on the reef (R. Winterbottom, personal communication). None of them are known as exclusive cave-dwellers, but they are permanent mesolithial residents, since all also occur in other mesolithial habitats, like small shallow caves and crevices (R. Winterbottom, personal communication). These species are very small and, as in the case of the Mediterranean *Tripterygion melanurus*, *T. minor* and *M. nigriceps*, most have a colouration pattern dominated by a red or orange colour.

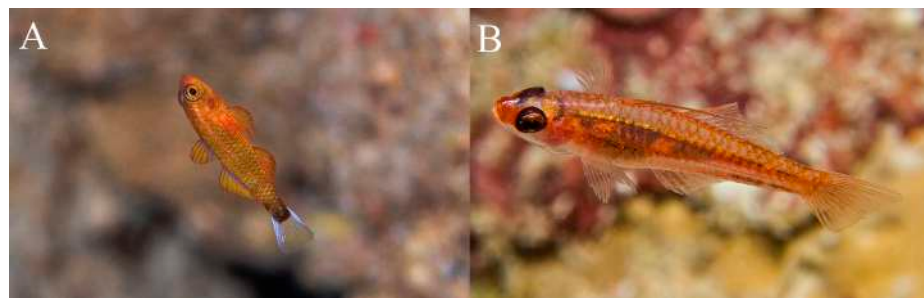


Figure 15. (A) *Trimma flavatrum* Hagiwara & Winterbottom, 2007, photo by K. Hagiwara. (B) *Trimma nubarum* Winterbottom, Bogorodsky & Alpermann, 2023, photo by S.V. Bogorodsky.

The bythitid *Grammonus ater* (Risso, 1810) (Figure 9B) is another Mediterranean cave inhabitant with a long history of published records, but with no positive published records outside marine caves [19]. This species has also been observed and collected from other mesolithial habitats by one of the authors (MKcollected material has been stored in the collection of the Natural History Museum Rijeka, Croatia) (Figure 9B). *Grammonus ater*, therefore, can be considered as a permanent and exclusive mesolithial resident, which does not inhabit other habitats and has never been recorded outside cryptic environments. In the Mediterranean Sea this species has been found in numerous marine caves from the Levantine Basin [115] to the Alboran Sea [116] (Table 2). Other *Grammonus* species were

also reported in littoral marine caves in other seas, such as West Pacific *Grammonus thielei* Nielsen & Cohen, 2004 and *Grammonus yunokawai* Nielsen, 2006 [83,84] and Hawaiian *Grammonus nagaredai* Randall & Hughes, 2008 [88]. Several species of Bythitidae, such as the above-mentioned *Grammonus* spp., occur in shallow water mesolithion; some are confined to brackish or freshwater, while others are deep-water fishes [117]. While brackish or freshwater Bythitidae from anchialine habitats show troglomorphic adaptation such as the loss of eyes and pigmentation, like *Typhlias pearsei* Hubbs, 1938 [118], the mesolithial littoral marine species have the typical adaptation of deep-water bythitids, having brown or black pigmentation and small eyes reduced in size [119]. The species *Protanguilla palau* Johnson, Ida & Sakaue 2012 (Figure 9A) has been described as a “living fossil” from a marine cave, as it represents the only fish family restricted to marine caves, the family Protanguillidae Johnson, Ida & Sakaue 2012. This species also has the adaptation of dark pigmentation and small eyes [89] (Figure 9A). It is possible, although still not recorded, that species like *P. palau* or *Grammonus ater* are nocturnal, leaving the caves to forage on the reef at night. Several species of Anguilliformes and Ophidiiformes reported by Hui et al. [90] in submarine and associated anchialine caves in Christmas Island (Indian Ocean Territory, Australia), also exhibit this body shape. The dark pigmentation and small eyes, combined with elongated snake-like body, resemble the fourth body type of adaptation to mesolithion, in addition to two body and colouration types of small cryptobenthic fish and one body and colouration type of small epibenthic fish. However, permanent and exclusive residents of mesolithial habitats share this body type with confirmed nocturnal species which spend the daytime in mesolithion but leave these shelters at night, therefore making them diel switchers between open sea floor spaces and mesolithial habitats, like *Gaidropsarus mediterraneus* (Linnaeus, 1758) (Figure 9C), and with eurybathic species recorded in marine caves, like *Ophidion barbatum* (Linnaeus, 1758) (Figure 9D).

In addition to the cryptobenthic and epibenthic fishes, which could be lifelong exclusive mesolithial residents, some Mediterranean hyperbenthic fishes are also exclusive permanent mesolithial residents. *Anthias anthias* (Figure 6C) was already considered to be an exclusive cave dweller by Abel [12] (Table 2). The species was indeed recorded at the cave entrances as well as inside caves, in semidark zones [71], being an exclusive permanent mesolithial resident. The rare records of *A. anthias* in the published studies about Mediterranean caves could possibly be due to the deep bathymetric range of *A. anthias*, down to 200 m depth [107], and the relatively shallow depth of most studied marine caves [17]. *Anthias anthias* shows the adaptation of large eyes for better vision in dimly lit habitats and red colouration for better camouflage against potential enemies in dim light. Based on the similar hyperbenthic fish adaptations of large eyes and red body colouration, the native Mediterranean *Callanthias ruber* (Rafinesque, 1810) is another candidate among hyperbenthic fishes of exclusive permanent mesolithial residents [107]. It occurs within a wide depth range (50–500 m) and has also been recorded from marine caves [120]. It is also possible that this is an exclusive mesolithial species in the upper circalittoral zone, and a species of open benthic environments in the lower circalittoral and bathyal zones, selecting the same photic condition along its depth range; however, there is no published evidence for this hypothesis. The adaptations of large eyes and red colouration on a typical hyperbenthic body that is tall and laterally compressed resembles the fifth type of body adaptation for life in the mesolithion. However, this body type is not restricted to permanent and exclusive mesolithial residents since it is shared with nocturnal species that spend the day in mesolithion and leave these shelters at night and, therefore, are diel switchers between open sea floor spaces and mesolithial habitats, like the Mediterranean cardinal fish *A. imberbis* (Figure 6A) [64,70,121] or the Indo-Pacific species *S. rubrum* (Figure 6D) [122]. Similar adaptations can be observed worldwide in some other fish families such as Apogonidae, Callanthidae (Figure 6C), Labridae, Holocentridae (Figure 6E), Priacanthidae (Figure 6F), Pseudochromidae (Figure 6B) and Serranidae of the subfamily Anthinae. Such species are rarely exclusive permanent mesolithial residents, like *Chlidichthys auratus* Lubbock, 1975 (Figure 6B), and the most mesolithial species of these

families for which the data exist are switchers between marine caves and open benthic environments or species also living at greater depths [91,94,95,120,123–125].

In addition to the five observed types of body adaptation for life in mesolithion, a number of permanent and exclusive mesolithial fish residents have various other body shapes and body colouration patterns. Some permanent and exclusive mesolithial residents show unique body shape and colouration, like the Mediterranean population of the epibenthic gobiid *Thorogobius ephippiatus* (Lowe, 1839) (Figure 16A), which has frequently been reported in microhabitats within larger cryptic spaces (e.g., marine caves), looking for thigmotactic shelters only when scared or chased (Table 2). Compared to the small earlier mentioned cryptobenthic and epibenthic fishes, this is a larger goby with striking dark flecked colouration. The seabed positioning and behaviour of *T. ephippiatus* in the Adriatic Sea was described by Kovačić [60].

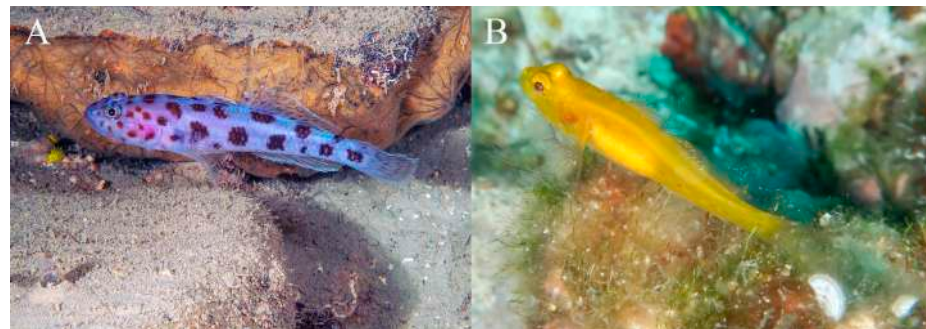


Figure 16. (A) *Thorogobius ephippiatus* (Lowe, 1839), photo by S. Guerrieri. (B) *Gobius auratus* Risso, 1810, photo by M. Kovačić.

Many small-sized benthic fishes can be considered as permanent, but not exclusive residents, of dimly sheltered large mesolithial habitats of caves and pseudocaves. They are also regularly recorded in other habitats, but due to their size, lifespan and behaviour, it is unlikely that the particular individual observed in caves and pseudocaves migrates to and from open benthic environments. These species show no adaptations for life in mesolithial habitats. For example, the Mediterranean gobiid *Gobius auratus* Risso, 1810 (Figure 16B) has been recorded at cave entrances and semidark zones inside caves [68] (Table 2). *Gobius auratus* usually hovers around a few to about 30 cm above the rocky or mixed substrate, especially juveniles in small schools, and can be easily noticed by its intensively yellow colouration [126] (Figure 16B). This goby, as well as several blenniid species [17,18,71] are permanent, but not exclusive, residents of marine caves since they are usually observed in open benthic environments, mostly as ambivalent fish [112,127].

3.2.4. Fishes as Accidental and Regular Visitors to Mesolithion and as Switchers between Mesolithion and Open Benthos

Abel [12] distinguished marine fishes that are occasional cave dwellers regularly visiting caves versus fishes which generally avoid caves despite having been recorded there. The Mediterranean examples in the latter category, based on Abel's records, were single individuals of neritic epipelagic *Belone* sp. juvenile and the hyperbenthic *Symphodus ocellatus* (Linnaeus, 1758). Other characteristic examples of accidental cave visitors are the previously mentioned benthopelagic *B. boops* and the epipelagic *S. dumerili* [71] (Table 2).

In contrast to accidental visitors, Abel [12] included, among the occasional cave dwellers that regularly visit marine caves, fishes dwelling around adjacent rocky beds, like *Coris julis* (Linnaeus, 1758), or which use caves as safe shelters (e.g., *Serranus* spp.), for reproduction (e.g., Blenniidae), or for hiding during the day- or night-time, such as *Muraena helena* Linnaeus, 1758 (Figure 17A) and groupers (Table 2). All these species can be considered as common mesolithial visitors or as switchers between mesolithion and open benthic environments. In addition to the time irregular visiting and to the diel hiding,

both noticed by Abel [12], the seasonal utilization and seasonal switching to mesolithial habitats of benthic fishes has also been observed in the Mediterranean Sea [128,129], and probably occur in other temperate seas. Single fish species can utilize marine caves in many of these ways, as diel or as seasonal switchers between mesolithion and open water or also as common visitors to marine caves for different reasons with no time regularity.

The only Mediterranean pomacentrid species, *Chromis chromis* (Linnaeus, 1758) (Figure 17B), is known to live in small shoals in midwater, above or near the sea floor, and to nest on the sea floor, with the juveniles reported as using cavities as shelters during the night [130] (Table 2). Quantitative cryptobenthic studies have revealed intensive use of cryptic spaces independently of the time of day, by both adult and juvenile *C. chromis* (Glavičić et al. [112] and references therein). The species is obviously a common switcher between hidden spaces and the water column and has also been recorded in marine caves *sensu stricto* [12].

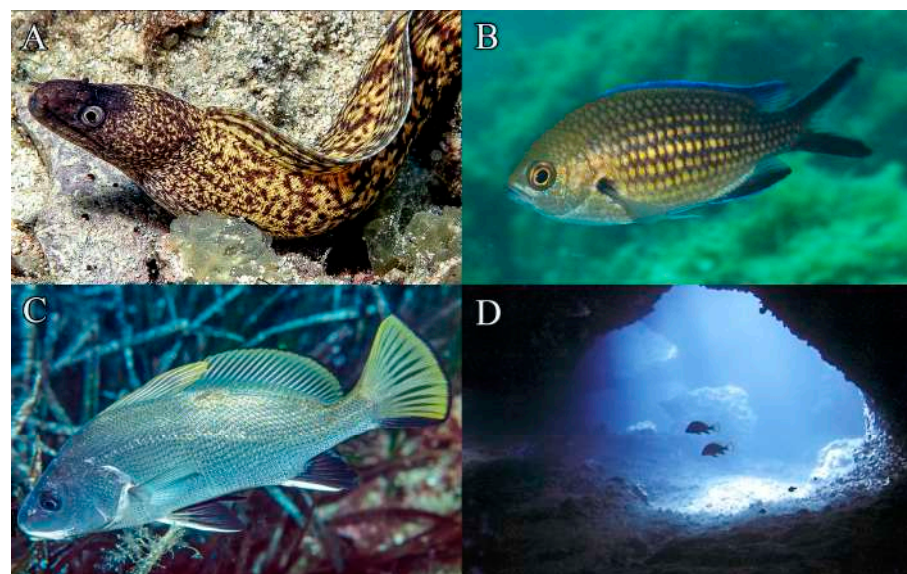


Figure 17. (A) *Muraena helena* Linnaeus, 1758; (B) *Chromis chromis* (Linnaeus, 1758); (C) and (D) *Sciaena umbra* Linnaeus, 1758. Photo (A,C,D): R.A. Patzner; (B): M. Kovačić.

The cardinal fish *A. imberbis* (Figure 6A), despite being reported from the dark deep zones of caves [71,121], was classified by Abel [12] as a switcher between marine caves and open benthic environments, using marine caves as a daytime hiding place and moving out from the caves at night to feed [12,13] (Table 2). The night shift of *A. imberbis* was recorded by Bussotti et al. [64]. Bussotti et al. [70,121] confirmed the existence of nycthemeral (diel) movements of this species to the outside of marine caves for feeding. The high densities of *A. imberbis* and its frequency of occurrence show that this species is by far the most represented fish within caves in the western Mediterranean [64,70]. Despite being the most characteristic fish in Mediterranean marine caves, this species is not an exclusive mesolithial resident. *Sargocentron rubrum* (Figure 6D) is also a diel switcher between open benthic environments and marine caves, leaving cave shelters at night to feed [13,81,82]. Both species have the adaptations of large eyes and red colouration on a typical hyperbenthic body that is tall and laterally compressed. Some larger fishes also show a preference for hidden spaces and occur in darker inner sections of marine caves during the day, such as the Mediterranean moray eel (*M. helena*) (Figure 17A), *C. conger*, *Phycis phycis* (Linnaeus, 1766), *Sciaena umbra* Linnaeus, 1758 (Figure 17C,D) or groupers (Table 2) [12,17]. Most of these fishes are nocturnal species which leave their shelters at night and, therefore, are diel switchers between open benthic environments and mesolithial habitats. The Indo-Pacific sweeper *Pempheris rhomboidea* (Figure 7D), an alien species in Mediterranean marine caves, is another diel switcher between open benthic environments and mesolithial habitats. It

shelters in large schools inside caves and crevices during the daytime and leaves them at night to feed [44,59,82]. The coelacanths in deep marine caves of the Indian Ocean occupied caves during the day but not at night [31,32]. After sunset coelacanths left their caves and moved or drifted one by one very slowly across the lava cliffs [32].

Similar body shape and colouration adaptation to *A. imberbis*, that also matches to one of the body adaptations described for the permanent residents in the mesolithion, can be found in species of several fish families in other seas, like Apogonidae, Holocentridae (Figure 6D,E), Priacanthidae (Figure 6F), Serranidae of subfamily Anthinae and Callanthidae. However, these species are nocturnal, leaving marine caves at night for feeding in open water and spending daytime in marine caves (Apogonidae, [94]; Holocentridae, [125] or they live at greater depths (Anthinae, [91]; Priacanthidae, [124]). Others are daytime feeders in open water, spending nights in marine caves and ranging from shallow to deeper zones (Callanthidae, [120]). Species of the Apogonidae, Holocentridae, Priacanthidae and Anthinae have also been recorded near and inside deep-water caves by Heemstra et al. [33], showing visiting or switching behaviour even at large depths.

Two larger mesolithial habitats, marine caves and pseudocaves, host additional fishes in winter. Kotrschal [128] observed that many Mediterranean Sparidae, Labridae, Serranidae and Pomacentridae turn from “facultative cave-dwellers” to “obligatory cave-dwellers” during the winter. He also recorded dense aggregations of *C. chromis* (Figure 17B) and *Oblada melanura* (Linnaeus, 1758) permanently remaining in caves during January and February. These mixed aggregations in marine caves may also consist of a few individuals of several species of the genus *Diplodus* Rafinesque, (Risso, 1810) as well as *Symphodus roissali* (Risso, 1810) and *C. julis*, with an interindividual distance of approximately 10 cm, and no aggressive behaviour or feeding having been observed (Table 2) [128,129].

Some fishes recorded both in marine caves and in open water are too small and static to be either visitors to marine caves or switchers between marine caves and open benthos. For the following examples of irregular, daily or seasonal utilization of cryptobenthic habitats by small fishes, the fishes at the cave entrance zone very likely do the same, while those that present deeper inside marine caves possibly also utilize “cave within cave” shelters in the similar way. Cryptobenthic habitats are very common and abundant on shallow benthic environments. Crevices in bedrock, interstitial spaces among boulders, pebbles and gravels or spaces produced by biocover [109] are commonly present in almost all rocky and/or mixed substrates. Almost every epibenthic fish and many hyperbenthic fishes of rocky and/or mixed substrates will eventually look for shelter in cryptic habitats when scared or chased and will therefore be mesolithial accidental visitors. Many small littoral benthic fishes which are not strictly cryptobenthic, were found in significant numbers during quantitative studies, either hidden or lying on the floor of Mediterranean marine caves (Glavičić et al. [112] and references therein), thus being more than just mesolithial accidental visitors. Various gobiid, blenniid and triplefin blennies were therefore classified as epicryptobenthic [109] or as ambivalent fishes, considering habitat positioning being regular mesolithial visitors or even common switchers between hidden spaces and the open benthic environment [112]. In the Adriatic Sea the occurrence frequencies of epicryptobenthic or ambivalent fishes did not change significantly between the time of day, and so no specific day- or night-time hiding was found for these fishes [112]. In addition, the cryptobenthic fish assemblage showed diel stability with no night-time presence in the open benthic environments [112]. However, some night visual censuses recorded the absence of blennies and tripterygiids, which were present at the same place during the daytime (e.g., Azzurro et al., [131]). This would indicate that fishes hide in the mesolithial shelters at night. Nieder and Zander [132] found nocturnal activity of *Lipophrys trigloides* (Valenciennes, 1836) outside shelters, presuming that all other Mediterranean blennies spend the night in holes. These findings indicate a possibility that some blenniids and tripterygiids are diel switchers between open benthic environments and cryptobenthic habitats. Abel [12] also presumed that holes were nighttime hiding places for Mediterranean blennies. Regarding seasonal utilization of cryptobenthic habitats, Kotrschal [128] recorded

the winter absence of the Mediterranean Blenniidae and Tripterygiidae on the surface of the substrate, while winter and summer Quinaldine collecting yielded similar numbers of blennies, tripterygiids and gobies over similar surface areas. Thus, he presumed that in the winter, the collected fish were hiding in holes and crevices, showing a seasonal switch to cryptobenthic habitats due to low temperatures. For instance, the Mediterranean *Tripterygion tripteronotus* (Risso, 1810), which never hides in crevices during the warm season, remains hidden during low temperatures [128]. Most gobies and blennies, which are the richest families among the Mediterranean epibenthic fishes in terms of species number [133], are also regular periodic dwellers in cryptobenthic habitats for longer, seasonal periods using the cryptic habitats as nests for their demersal eggs [134,135]. Abel [12] also noticed this for Mediterranean blennies and tripterygiids. Most Mediterranean blennies utilize the empty holes of endolithic bivalves as mesolithial nests [135]. Therefore, epibenthic gobies and blennies are seasonal switchers to cryptobenthic habitats for their reproductive needs. The seasonal presence of blennies inside holes in spring can be explained as a feature of nest dwelling.

3.3. The Biodiversity of Fishes in Marine Caves and Their Relationship to Marine Caves

Fishes recorded in marine caves constitute only a minute fraction of the total fish diversity in most marine areas of the world, probably due to the limited research effort and knowledge (see Sections 3.1 and 3.2). In this sense, it is astonishing that a total of 132 fish species have been recorded so far from the Mediterranean marine caves *sensu stricto* [9,18,82,136] (Table 2 and references therein), representing about 17% of the total Mediterranean marine fish diversity and approximately one third of the Mediterranean littoral benthic fish species [133,137] (Table 2). Only 3.0% are neritic epipelagic fishes and 4.5% are benthopelagic (Table 2). All benthic species (except one) occur in the infralittoral zone, with different depth tolerances ranging from strict infralittoral species (37.1%) to species occurring in infralittoral and circalittoral zones (40.2%) and eurybathic species, which occur from the infralittoral to the bathyal zone (14.4%). A single species (0.8%), *Callanthias ruber*, is known from circalittoral to bathyal waters (Table 2). Regarding the position to the sea floor, counting only the recorded benthic fishes, most species among benthic fishes are hyperbenthic (49.2%) and epibenthic (38.5%), while 12.3% are cryptobenthic (Table 2).

A total of 43 families are represented in Mediterranean marine caves. Most species belong to the families Gobiidae (20 species), Blenniidae (14 species), Labridae (13 species), Sparidae (12 species), Serranidae (9 species) and Scorpaenidae (6 species), while the remaining families include less than five species each (25 families include only one species). Most species have been reported from the entrance and semidark zones of the studied marine caves (91 and 76 species, respectively), while only 34 species have been recorded in dark cave zones. For 17 fish species there is no information concerning the cave zone where they were recorded. Gobiidae is the most speciose family in the two anterior cave zones (15 and 12 species, respectively), followed by Blenniidae at the entrance and Sparidae at the semidark zone (13 and 10 species, respectively). Most species reported from the dark zone of caves belong to the families Serranidae (6 species), Gobiidae and Scorpaenidae (5 species each). While the most speciose families are the same in all cave zones, Blenniidae disappear completely from the dark cave zone.

We classified fishes recorded in the Mediterranean marine caves as: (a) exclusive permanent residents of mesolithial habitats (based on references in Sections 3.1 and 3.2; Glavičić et al. [112] and references therein); (b) mesolithion permanent residents whose populations also occur in other habitats, but do not migrate (based on data in Bussotti et al. [17] and Kovačić et al. [18]); (c) regular mesolithion visitors and switchers between mesolithion and open water with temporal regularity (based on data in Kotschal [128], Kotschal and Reynolds [129], Kotschal [135], Glavičić et al. [112] and references therein). The species with no published information regarding their relationship to the mesolithion were assigned based on the authors' judgement and unpublished experience. Among

the 132 fish species recorded in the Mediterranean marine caves *sensu stricto*, 27.3% are accidental visitors in the mesolithion, 53.8% are regular mesolithial visitors and switchers between mesolithion and open water, 5.3% are mesolithial permanent residents whose populations also occur in other habitats; and 13.6% are mesolithial exclusive permanent residents (Table 2). These estimates are conservative, selecting the minimum strength of the fish relationship to the mesolithion, where no other evidence was available. For example, fishes of pelagic and sandy habitats were presumed to be accidental visitors in the mesolithion, in the absence of other evidence. Therefore, it could be expected that with increasing knowledge, the proportion of the species with stronger relationships to mesolithial habitats would also increase. Among the 18 exclusive permanent mesolithial resident fishes recorded in Mediterranean marine caves, one has a snake-like body, dark pigmentation and small eyes (*G. ater*, Figure 9B), two have laterally compressed bodies with large eyes and red colouration (*A. anthias*, Figure 6C and *C. ruber*), and three have small, slender bodies and red or orange colouration pattern (*M. nigriceps*, *T. melanurus*, *T. minor*) (Figure 10) (Table 2). Five species are small-sized fish with robust bodies and large heads (Figure 13) and five have small, elongated bodies and flattened heads (Figure 14) (Table 2). The remaining two exclusive permanent residents, *Scorpaenodes arenai* Torchio, 1962 and *T. ephippiatus* (Figure 16A), did not match any of these body types, and the data on *S. arenai* are very scarce (Table 2).

Table 2. Fishes recorded in Mediterranean marine caves. The data on cave zones are from published sources cited in this present work and from personal observations of the authors. Marine cave zones (if known): CE—cave entrance; SD—semidark zone; D—dark zone. The data about marine environments, depth zones and the position of benthic fishes to the bottom are based on Froese and Pauly [111] and Dulčić and Kovačić [107]. Categories for environments and depth zones: I—infra-littoral; IC—infra-littoral and circalittoral; ICB—infra-littoral, circalittoral and bathyal; CB—circalittoral and bathyal; B—benthopelagic; NE—neritic epipelagic. Categories for position of benthic fish to the sea floor: Hb—hyperbenthic; Eb—epibenthic; Cb—cryptobenthic. See Table 1 for the categories for relationship of fishes to mesolithial habitats and Section 3.3 for data sources.

Species	First References in Mediterranean Marine Caves	Cave Zone			Environment and Depth Zone	Position to the Sea Floor	Relationship to Mesolithial Habitats
		CE	SD	D			
<i>Acantholabrus palloni</i> (Risso, 1810)	[55]	+			IC	Hb	2
<i>Aidablennius sphynx</i> (Valenciennes, 1836)	[80]	+			I	Eb	2
<i>Anthias anthias</i> (Linnaeus, 1758)	[12]	+	+	+	ICB	Hb	4
<i>Apogon imberbis</i> (Linnaeus, 1758)	[39]	+	+	+	ICB	Hb	3
<i>Apogonichthyoides pharaonis</i> (Bellotti, 1874)	[138]	+			IC	Hb	2
<i>Atherina boyeri</i> Risso, 1810	[139]	+	+		B	/	1
<i>Atherinomorus forskalii</i> (Rüppell, 1838)	[140]	+			B	/	1
<i>Atherinomorus lacunosus</i> (Forster, 1801)	[140]	+	+		B	/	1
<i>Bathytoshia centroura</i> (Mitchill, 1815)	[17]				ICB	Eb	2
<i>Belone belone</i> (Linnaeus, 1761)	[13]				NE	/	1
<i>Boops boops</i> (Linnaeus, 1758)	[141]	+	+		B	/	1
<i>Bothus podas</i> (Delaroche, 1809)	[142]		+		ICB	Eb	1
<i>Callanthias ruber</i> (Rafinesque, 1810)	[120]				CB	Hb	4
<i>Cheilodipterus novemstriatus</i> (Rüppell, 1838)	[143]	+	+		IC	Hb	2
<i>Chelon</i> sp.	[67]	+	+		I	Hb	1
<i>Chromis chromis</i> (Linnaeus, 1758)	[12]	+	+		I	Hb	2
<i>Chromogobius quadrivittatus</i> (Steindachner, 1863)	[13]	+			I	Cb	4
<i>Chromogobius zebratus</i> (Kolombatović, 1891)	[80]	+	+		I	Cb	4
<i>Conger conger</i> (Linnaeus, 1758)	[41]	+	+	+	IC	Cb	2
<i>Coryrogobius liechtensteini</i> (Kolombatović, 1891)	[52]	+	+	+	IC	Cb	4
<i>Coris julis</i> (Linnaeus, 1758)	[12]	+	+	+	IC	Hb	2
<i>Coryphoblennius galerita</i> (Linnaeus, 1758)	[80]	+			I	Eb	2
<i>Ctenolabrus rupestris</i> (Linnaeus, 1758)	[70]				IC	Hb	2
<i>Dasyatis pastinaca</i> (Linnaeus, 1758)	[79]		+		IC	Eb	2
<i>Dicentrarchus labrax</i> (Linnaeus, 1758)	[144]	+			IC	Hb	1
<i>Diplodus annularis</i> (Linnaeus, 1758)	[62]	+	+		IC	Hb	2
<i>Diplodus puntazzo</i> (Walbaum, 1792)	[145]		+		IC	Hb	2
<i>Diplodus sargus</i> (Linnaeus, 1758)	[12]	+	+		IC	Hb	2
<i>Diplodus vulgaris</i> (Geoffroy Saint-Hilaire, 1817)	[12]	+	+	+	IC	Hb	2
<i>Enchelycore anatina</i> (Lowe, 1838)	[146]	+	+	+	IC	Eb	2
<i>Epinephelus aeneus</i> (Geoffroy Saint-Hilaire, 1817)	[147]				IC	Hb	2
<i>Epinephelus caninus</i> (Valenciennes, 1843)	[12]		+		ICB	Hb	2
<i>Epinephelus costae</i> (Steindachner, 1878)	[68]	+	+	+	ICB	Hb	2
<i>Epinephelus marginatus</i> (Lowe, 1834)	[12]	+	+	+	ICB	Hb	2
<i>Fistularia commersonii</i> Rüppell, 1838	[140]	+			IC	Hb	1

Table 2. Cont.

Species	First References in Mediterranean Marine Caves	Cave Zone			Environment and Depth Zone	Position to the Sea Floor	Relationship to Mesolithial Habitats
		CE	SD	D			
<i>Gaidropsarus mediterraneus</i> (Linnaeus, 1758)	[139]		+		ICB	Cb	2
<i>Gammogobius steinitzi</i> Bath, 1971	[42]	+	+	+	IC	Cb	4
<i>Gobius auratus</i> Risso, 1810	[148]		+		I	Eb	3
<i>Gobius bucchichi</i> Steindachner, 1870	[13]	+			I	Eb	2
<i>Gobius cobitis</i> Pallas, 1814	[80]	+			I	Eb	2
<i>Gobius cruentatus</i> Gmelin, 1789	[149]	+			I	Eb	3
<i>Gobius geniporus</i> Valenciennes, 1837	[62]	+			I	Eb	2
<i>Gobius niger</i> Linnaeus, 1758	[13]		+	+	IC	Eb	2
<i>Gobius paganellus</i> Linnaeus, 1758	[80]	+			I	Eb	2
<i>Gobius vittatus</i> Vinciguerra, 1883	[149]	+	+		IC	Eb	2
<i>Gouania willdenowi</i> (Risso, 1810)	[13]	+			I	Cb	4
<i>Grammonus ater</i> (Risso, 1810)	[13]			+	I	Cb	4
<i>Hemiramphus far</i> (Fabricius 1775)	[147]				NE	/	1
<i>Labrus merula</i> Linnaeus, 1758	[128]	+			I	Hb	2
<i>Labrus mixtus</i> Linnaeus, 1758	[13]	+	+	+	IC	Hb	2
<i>Lepadogaster candolii</i> Risso, 1810	[145]		+		I	Cb	4
<i>Lepadogaster lepadogaster</i> (Bonnaterre, 1788)	[13]			+	I	Cb	4
<i>Lipophrys trigloides</i> (Valenciennes, 1836)	[12]	+			I	Eb	2
<i>Lithognathus mormyrus</i> (Linnaeus, 1758)	[142]		+		IC	Hb	1
<i>Marcelogobius splechnai</i> (Ahnelt & Patzner, 1995)	[51]		+	+	IC	Cb	4
<i>Microlipophrys canevae</i> (Vinciguerra, 1880)	[12]	+			I	Eb	2
<i>Microlipophrys dalmatinus</i> (Steindachner & Kolombatović, 1883)	[12]	+			IC	Eb	2
<i>Microlipophrys nigriceps</i> (Vinciguerra, 1883)	[12]	+	+		I	Cb	4
<i>Mugil cephalus</i> Linnaeus, 1758	[13]				I	Hb	1
<i>Mullus barbatus</i> Linnaeus, 1758	[142]		+		IC	Hb	1
<i>Mullus surmuletus</i> Linnaeus, 1758	[63]	+	+	+	ICB	Hb	1
<i>Muraena helena</i> Linnaeus, 1758	[12]	+	+	+	IC	Eb	2
<i>Mycteroperca rubra</i> (Bloch, 1793)	[79]	+	+		IC	Hb	2
<i>Neogobius melanostomus</i> (Pallas, 1814)	[13]				I	Eb	1
<i>Oblada melanura</i> (Linnaeus, 1758)	[12]	+	+	+	IC	Hb	2
<i>Odondebuena balearica</i> (Pellegrin & Fage, 1907)	[18]		+		IC	Cb	4
<i>Ophidion barbatum</i> Linnaeus, 1758	[17]				ICB	Cb	3
<i>Pagrus caeruleostictus</i> (Valenciennes, 1830)	[79]		+	+	IC	Hb	1
<i>Parablennius gattorugine</i> (Linnaeus, 1758)	[12]	+	+		I	Eb	2
<i>Parablennius incognitus</i> (Bath, 1968)	[145]	+			I	Eb	2
<i>Parablennius pilicornis</i> (Cuvier, 1829)	[74]	+			I	Eb	2
<i>Parablennius rouxi</i> (Cocco, 1833)	[12]	+	+		I	Eb	3
<i>Parablennius sanguinolentus</i> (Pallas, 1814)	[140]	+			I	Eb	2
<i>Parablennius tentacularis</i> (Brünnich, 1768)	[17]		+		I	Eb	3
<i>Parablennius zvonimiri</i> (Kolombatović, 1892)	[12]	+	+		I	Eb	3
<i>Parupeneus forsskali</i> (Fourmanoir & Guézé, 1976)	[79]	+	+		IC	Eb	1
<i>Pempheris rhomboidea</i> Kossmann & Räuber, 1877	[44]	+	+	+	IC	Hb	2
<i>Phycis phycis</i> (Linnaeus, 1766)	[149]	+	+	+	ICB	Hb	2
<i>Plotosus lineatus</i> (Thunberg, 1787)	[150]				IC	Hb	2
<i>Polyprion americanus</i> (Bloch & Schneider, 1801)	[13]				ICB	Hb	2
<i>Pomatoschistus adriaticus</i> Miller, 1973	[43]		+		I	Eb	1
<i>Pterois miles</i> (Bennett, 1828)	[150]	+	+	+	IC	Eb	2
<i>Salaria pavo</i> (Risso, 1810)	[12]	+			I	Eb	2
<i>Sargocentron rubrum</i> (Forsskål, 1775)	[13]	+	+	+	IC	Hb	2
<i>Sarpa salpa</i> (Linnaeus, 1758)	[71]	+			I	Hb	1
<i>Sciaena umbra</i> Linnaeus, 1758	[12]	+	+	+	ICB	Hb	2
<i>Scorpaena maderensis</i> Valenciennes, 1833	[17]	+	+		ICB	Eb	2
<i>Scorpaena notata</i> Rafinesque, 1810	[12]	+	+	+	ICB	Eb	2
<i>Scorpaena porcus</i> Linnaeus, 1758	[12]	+	+	+	IC	Eb	2
<i>Scorpaena scrofa</i> Linnaeus, 1758	[41]	+	+	+	IC	Eb	2
<i>Scorpaenodes arenai</i> Torchio, 1962	[151]		+		IC	Eb	4
<i>Scyliorhinus</i> sp.	[41]			+	ICB	Hb	1
<i>Seriola dumerili</i> (Risso, 1810)	[71]	+	+		NE	/	1
<i>Serranus cabrilla</i> (Linnaeus, 1758)	[39]	+	+	+	IC	Hb	2
<i>Serranus hepatus</i> (Linnaeus, 1758)	[62]	+	+	+	IC	Hb	2
<i>Serranus scriba</i> (Linnaeus, 1758)	[12]	+	+	+	IC	Hb	2
<i>Siganus luridus</i> (Rüppell, 1829)	[138]	+	+		I	Hb	1
<i>Siganus rivulatus</i> Forsskål & Niebuhr, 1775	[138]	+			I	Hb	1
<i>Solea solea</i> (Linnaeus, 1758)	[67]			+	IC	Eb	1
<i>Sparisoma cretense</i> (Linnaeus, 1758)	[71]	+			IC	Hb	2
<i>Sparus aurata</i> Linnaeus, 1758	[145]	+			IC	Hb	1
<i>Speleogobius trigloides</i> Zander & Jelinek, 1976	[43]	+	+		IC	Eb	3
<i>Sphyræna pinguis</i> Günther, 1874	[138]				IC	Hb	1
<i>Sphyræna viridensis</i> Cuvier, 1829	[68]		+		IC	Hb	1
<i>Spicara maena</i> (Linnaeus, 1758)	[65]	+	+		B	/	1
<i>Spicara smaris</i> (Linnaeus, 1758)	[18]	+	+		B	/	1
<i>Stephanolepis diaspros</i> Fraser-Brunner, 1940	[150]				IC	Hb	2
<i>Symphodus doderleini</i> Jordan, 1890	[144]	+			I	Hb	1
<i>Symphodus mediterraneus</i> (Linnaeus, 1758)	[141]	+	+		I	Hb	2
<i>Symphodus melanocercus</i> (Risso, 1810)	[145]				I	Hb	2
<i>Symphodus ocellatus</i> (Linnaeus, 1758)	[12]	+			I	Hb	2
<i>Symphodus roissali</i> (Risso, 1810)	[129]	+			I	Hb	2
<i>Symphodus rostratus</i> (Bloch, 1791)	[141]	+			I	Hb	2
<i>Symphodus tinca</i> (Linnaeus, 1758)	[141]	+	+		I	Hb	2

Table 2. Cont.

Species	First References in Mediterranean Marine Caves	Cave Zone			Environment and Depth Zone	Position to the Sea Floor	Relationship to Mesolithial Habitats
		CE	SD	D			
<i>Thalassoma pavo</i> (Linnaeus, 1758)	[12]	+	+		I	Hb	2
<i>Thorogobius ephippiatus</i> (Lowe, 1839)	[13]	+	+	+	IC	Eb	4
<i>Thorogobius macrolepis</i> (Kolombatović, 1891)	[62]	+	+		I	Eb	2
<i>Torpedo marmorata</i> Risso, 1810	[152]			+	ICB	Eb	1
<i>Torquigener flavimaculosus</i> Hardy & Randall, 1983	[138]	+	+		IC	Hb	1
<i>Trachinus draco</i> Linnaeus, 1758	[144]	+			IC	Eb	1
<i>Trachurus trachurus</i> (Linnaeus, 1758)	[17]				NE	/	1
<i>Tripterygion delaisi</i> Cadenat & Blache, 1970	[43]	+	+		I	Eb	2
<i>Tripterygion melanurus</i> Guichenot, 1850	[153]				I	Cb	4
<i>Tripterygion minor</i> Kolombatović, 1892	[12]	+	+		I	Cb	4
<i>Tripterygion tripteronotum</i> (Risso, 1810)	[12]	+	+		I	Eb	2
<i>Trisopterus capelanus</i> (Lacepède, 1800)	[17]				ICB	Hb	2
<i>Umbrina cirrosa</i> (Linnaeus, 1758)	[13]		+		IC	Hb	2
<i>Upeneus moluccensis</i> Bleeker, 1855	[138]				IC	Hb	1
<i>Upeneus pori</i> Ben-Tuvia & Golani, 1989	[150]	+			IC	Hb	1
<i>Zebrus zebrus</i> (Risso, 1827)	[145]	+			I	Cb	4
<i>Zeugopterus regius</i> (Bonnaterre, 1788)	[62]		+		IC	Eb	0

3.4. The Distribution of Fishes in Marine Caves

Available studies concerning fishes in marine caves outside the Mediterranean Sea rarely include data on the distribution of fishes in marine caves and their relationship to the environmental and biological gradients (see Section 3.1). Micael et al. [97] distinguished a submarine tunnel in the Azores in the two entrance zones, two twilight zones and one middle dark zone and divided fishes according to their presence along these zones in the tunnel. Lam et al. [87] provided notes on the cave position for each fish species in the Conic Island Cave of Hong Kong. Specific information about the relationship of fishes to the biological community of the marine caves is absent even in cases where the fishes had been listed as part of the described biological community [90,93,100].

The more detailed studies of the distribution of fishes in marine caves and their relationship to the environmental and biological gradients have been published only for the Mediterranean. Zander and Jelinek [43] were the first to provide detailed information on the distribution of fishes inside caves and their relationship to light. They distinguished five biological zones within the cave Banjole (Croatia, Adriatic Sea) following Riedl's [13] zonation and recorded the presence and estimated abundance of several fish species along the light gradient. However, the fifth "darkest" zone was rather semidark, being inhabited with anthozoan *Parazoanthus* sp. and fishes such as *Parablennius zvonimiri* (Kolombatović, 1892) and *Parablennius gattorugine* (Linnaeus, 1758) [43]. Arko-Pijevac et al. [62] studied biocenoses of a long submarine cave at the island of Krk (Croatia, Adriatic Sea) and recorded fish from the coralligenous biocoenosis of the cave entrance, over the semidark middle part and to the completely dark cave interior. The number of recorded fish species decreased with the distance from the entrance [62]. However, in the deepest part of the cave they recorded the exclusive mesolithial permanent residents *G. steinitzi* (Figure 7C) and *T. ephippiatus* (Figure 16A) as well as some hyperbenthic regular visitors, namely *Labrus mixtus* Linnaeus, 1758, *Serranus hepatus* (Linnaeus, 1758) and *Serranus scriba* (Linnaeus, 1758) [62].

Reviewing all published data from the Mediterranean Sea, it is clear that the numerous fish species were recorded at the entrances and at the semidark zones of caves [17,18,62,68–71]. Records of fish species in the completely dark zones of posterior cave sections are quite rare for very long or bended caves [67]. The only fish species recorded at the inner part of the Y-Cave in the central Adriatic Sea (90 m long) was the speleophilic species *G. ater* [72], in contrast to the shorter marine caves at Vrbnik (30 m long) where several fish species occur in the innermost dark zones [62].

Larger or hyperbenthic fishes have also been reported from the dark sections of other Mediterranean marine caves such as *A. imberbis* (Figure 6A), *C. conger*, *C. chromis* (Figure 17B), *Diplodus vulgaris* (Geoffroy Saint-Hilaire, 1817), *Epinephelus costae* (Steindachner, 1878), *P. phycis*, *S. scriba* and *Serranus cabrilla* (Linnaeus, 1758) [63,71]. Among introduced fishes, *Enchelycore*

anatina (Lowe, 1838), *P. rhomboidea*, *Pterois miles* (Bennett, 1828) and *S. rubrum* were also recorded in the dark zone of Mediterranean marine caves [82].

In addition to *G. ater*, several small epibenthic and cryptobenthic fishes were regularly reported in the innermost sections of marine caves with poor or no light in the Mediterranean Sea, all belonging to the family Gobiidae: *C. liechtensteini* (Figure 13B), *M. splechnai* (Figure 13D), *G. steintzi* (Figure 7C), *T. ephippiatus* (Figure 16A) and *T. macrolepis* [18,19,62,68,73]. Other small mesolithial fishes belonging to the families Blenniidae, Gobiesocidae, Gobiidae and Tripterygiidae have been found in marine caves, though usually in shallow depths with more light or just at cave entrances, along with larger hyperbenthic fishes [14,62,68]. Among these species, regular inhabitants of the cave interior occupy two different microhabitats: bedrock ceilings and walls (*C. liechtensteini* and *G. steintzi*) (Figures 7C and 13B) or fine sediment of the cave floor (*M. splechnai*) (Figure 13D) [19,52,73]. As mentioned before, some of small fishes use holes and crevices in cave ceilings and walls, also known as “caves within caves” [12,18]. Zander [14] reported a “cryptophilic to acrophilic shift” for some small cryptic gobiids in marine caves which appear closer to the entrance cave zone with increasing water depth and decreasing light. This was also observed for *T. ephippiatus* (Figure 16A) by Kovačić [60] and for *C. liechtensteini* by Herler et al. [52].

4. Discussion

Fishes in marine caves have been rarely investigated; most of the available studies took place in the Mediterranean Sea (see Section 3.1 for the details). In addition, marine fishes were rarely mentioned in existing reviews about subterranean fishes [2,154] or were presented as a short summary with only a few references [1]. For example, Romero [155] mentioned only a single example about fishes in marine caves. Nevertheless, research efforts devoted to marine cave fishes has increased over the last few decades (see Section 3.1 for the details).

Marine cave fishes are taxonomically and phylogenetically distinct when compared to subterranean fishes from freshwaters and/or anchialine systems, except for anchialine and marine species of the genera *Lucifuga* (family Bythitidae) and *Ogilbia* (family Dinematchthyidae). Others are, at best, related at the family level to stygobitic species, such as those of the families Gobiidae and Anguillidae which occur in anchialine [5,156] and freshwater subterranean habitats [16]. Furthermore, no shared adaptations were found between fishes in marine caves and stygobitic species, although some reef dwellers of the family Dinematchthyidae and some burrowing Gobiidae species are shallow marine species but evolved troglomorphic adaptations, according to Proudlove [16]. Also, non-stygobitic fishes in freshwater subterranean habitats show no adaptations such as any of those presented in this work for the exclusive permanent residents of mesolithial habitats. Clearly, marine caves, with their strong connections with the open marine environment and rich sessile benthic communities, represent quite a different evolutionary challenge for fishes, when compared to subterranean freshwaters and anchialine systems. Consequently, this has resulted in quite different adaptation outcomes.

Many exclusive permanent residents of mesolithial habitats, which were recorded in marine caves, as well as regular visitors and switchers to marine caves, show no obvious shared colouration or morphological characteristics and maintain a similar appearance to fishes from open environments (Figure 7A,D). Some of them exhibit intraspecific “cryptophilic to acrophilic shift” *sensu* Zander [14]. *Centropyge colini* Smith-Vaniz & Randall, 1974 (family Pomacanthidae) was observed to occupy reefs at depth of 100 m or more, while also found in marine caves in depths less than 30 m (R. Pyle, personal communication). However, five types of morphological and colouration adaptations can be noticed among Mediterranean exclusive permanent residents of mesolithial habitats that were recorded in marine caves (Section 3.2.3). The two morphological types adapted for life in cryptobenthic habitats and recorded in marine caves (i.e., small body size with stout body and large head; and small, elongated body with flattened head) are common in various marine cryptobenthic habitats of the Mediterranean Sea (see examples in Section 3.2.3) but can also be found in other

oceans and seas. Such are the gobies of genus *Priolepis* Valenciennes, 1837, for the first body type, or the gobies of genus *Callogobius* Bleeker, 1874, for the second body type [157,158]. The adaptation type of small, slender and mostly uniformly red or orange-coloured body exists in fishes in marine caves which lie or hover over the cave bed, on cave walls or below ceilings, protected primarily by their poorly visible colouration in low blue light instead of hiding in holes and hollows for protection (Figures 10 and 15). It could be expected that this adaptation (mainly colour) also occurs in the low-light conditions of circalittoral and mesophotic depths, with a possible “cryptophilic to acrophilic shift” of these species with increasing depth [14]. However, congeneric species of marine cave residents which occur in mesophotic depths (e.g., some species of *Trimma*), are more yellow to orange than orange to red coloured, such as *Trimma citrum* Winterbottom & Pyle, 2022 [159]. These minor colour differences are probably irrelevant to the fishes, since red colour disappears by about 10 m, followed rapidly by orange and yellow. Thus, none of those colours are visible in the natural light of *Trimma* habitats. However, small fishes from deep, low-light habitats in the Mediterranean circalittoral and in the mesophotic zone of the western Atlantic, exhibit mostly yellow to orange colouration with a rather spotted, striped or marbled than uniform pattern (Figure 18) [160,161]. This colouration pattern is rarely present in low-light conditions inside “real” marine caves in shallow waters. In contrast, another type of body shape adapted to mesolithion, specifically dark pigmentation, small eyes and snake-like body (Figure 9), is shared between marine cave species and deep-water species of Anguilliformes and Ophidiiformes, with some species occurring down to 2,500 m depth, such as *Thermichthys hollisi* (Cohen, Rosenblatt & Moser, 1990) [156]. This species’ appearance looks to be the genuine deep-water adaptation that is also found in a small number of species of shallow marine caves. Furthermore, some of these fishes that are not permanent residents of mesolithion but are nocturnal species spending daytime in mesolithial habitats and leaving their shelters at night (e.g., *G. mediterraneus*, Figure 9C), are eurybathic, being present from infralittoral to bathyal depths [107]. Finally, large eyes and red colouration on fishes with a typical hyperbenthic body (laterally compressed) are common adaptations among fishes recorded in marine caves, including both those that are exclusive permanent residents of mesolithial habitats and those which are daily switchers and feed in the open water at night (Figure 6). This body type is also common among eurybathic species which reach deep, low-light benthic habitats, and also among species exclusively preferring deeper benthos. However, for most of these species, it remains unclear to what degree they use and they are dependent on marine cave habitats, especially with increasing depth (e.g., caves in mesophotic environments and if they exhibit intraspecific “cryptophilic to acrophilic shift” *sensu* Zander [14]). For example, according to observations, the red-coloured deep-sea species *Symphysanodon octoactinus* Anderson, 1970, *Symphysanodon berryi* Anderson, 1970 (family Symphysanodontidae), *Liopropoma* spp. (family Liopropomatidae), *Gonioplectrus hispanus* (Cuvier, 1828), and *Jeboehlkia gladifer* Robins 1967 (family Epinephelidae), often disappeared into caves and crevices when illuminated by the lights of a submersible (C. Baldwin, personal communication). In any case, the described body adaptation seems to be quite successful since it is shared by numerous fish species in mesolithion, and it is also widespread among fish species of different fish families in dim light conditions in general (see Sections 3.2.3 and 3.2.4 for details).

There is no Mediterranean fish species that is an exclusive dweller of marine caves and has not also been found in the other mesolithial habitats (see Sections 3.2.3 and 3.2.4 for details). Also, in other seas, the fish species found and described at the innermost part of the caves, like *Pseudamia zonata* Randall, Lachner & Fraser, 1985 (R. Winterbottom, personal communication), were later found in other habitats as well. *Pseudamia zonata* in particular is now known to hover in front of caves at night in depths of 10–30 m [162].

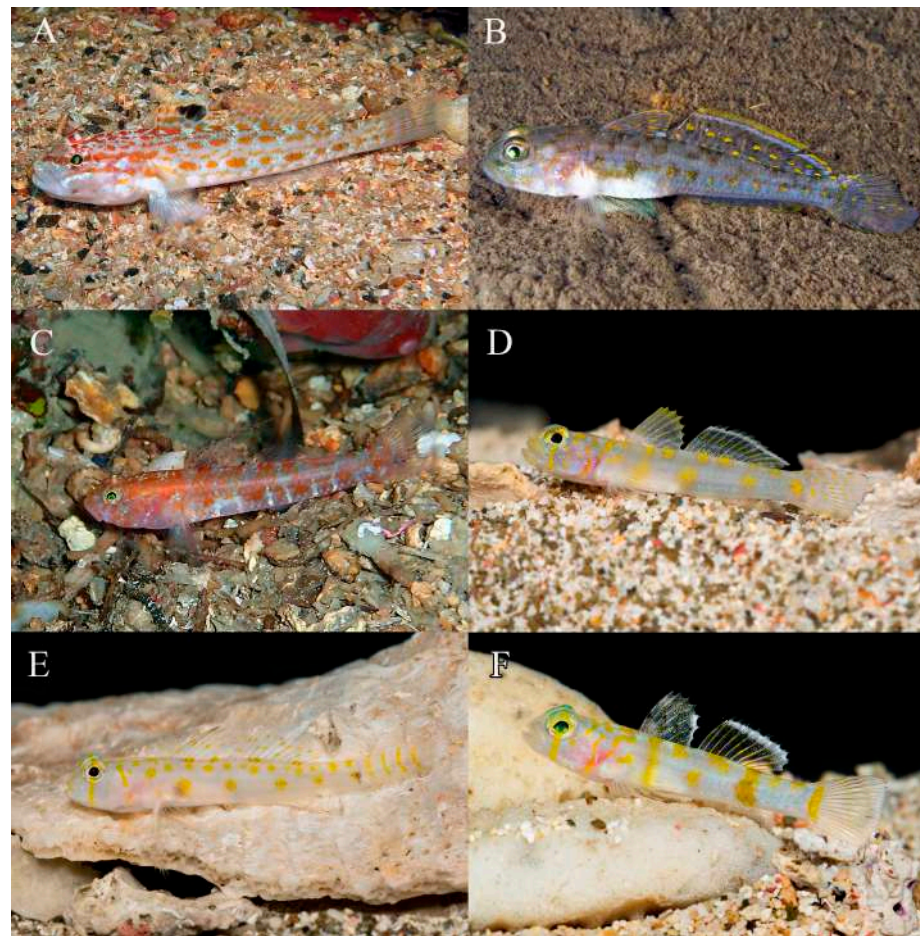


Figure 18. (A) *Gobioides kolombatovici* Kovačić & Miller, 2000, photo by S. Le Bris. (B) *Lesueurigobius friesii* Malm, 1874, photo by R. Svensen. (C) *Vanneaugobius dollfusi* Brownell, 1978, photo by S. Le Bris. (D) *Varicus cephalocellatus* Van Tassell, Baldwin & Gilmore 2016, (E) *Varicus decorum* Van Tassell, Baldwin & Gilmore 2016, (F) *Varicus veliguttatus* Van Tassell, Baldwin & Gilmore 2016, photos (D–F) by B.B. Brown (coralreefphotos) and C. Baldwin.

5. Conclusions

Marine caves constitute part of mesolithial habitats, together with pseudocaves (e.g., large crevices and overhanging rocks) and cryptobenthic habitats (i.e., living spaces underneath the bottom surface of the substrate or biocover, with a physical barrier to the open spaces). They are characterized by dim light conditions, low hydrodynamic regime and their rocky surfaces are usually dominated by sessile filter feeders (e.g., sponges and bryozoans).

Fishes in marine caves constitute an unexplored component of marine fish diversity, except for the relatively well-studied Mediterranean Sea. Relevant studies outside the Mediterranean Sea are restricted mostly to taxonomy and simple species lists. The fishes recorded in marine caves are not exclusive residents of these habitats and are also present in the other types of mesolithial habitats. More specifically, marine caves are inhabited by accidental and regular mesolithial visitors, switchers between mesolithion and open water, permanent mesolithial residents whose populations also occur in other habitats but do not migrate, and finally, by exclusive permanent mesolithial residents. Some mesolithial visitors show no regularity in the time of their visits, while others are daily or seasonal switchers between mesolithion and open water. A single fish species can use marine caves in more than one of the above ways. There is no fish species known to be exclusive marine cave dwellers that is not also found in the other mesolithial habitats or that is not a diel switcher occurring outside caves at night.

Unlike anchialine or freshwater caves, fishes with troglomorphic adaptation of eyes and pigmentation loss do not exist in marine caves. However, among the exclusive permanent mesolithial residents, in addition to the various other body shapes and colourations found in these fishes, we have identified five different morphological types related to the adaptation to mesolithial habitats.

A unique phenomenon in marine caves is the presence of small fishes occupying “cave within cave” niches (i.e., small hidden spaces open to inside larger marine cave volumes). Due to the lack of data, the relationship of fishes to deep marine caves and eventual shifts in the use of marine caves with increasing depth and decreasing light, is still unknown.

In the relatively well-studied Mediterranean Sea, fishes recorded in marine caves represent a considerable part (17%) of the total marine fish species richness. Among the 132 fish species recorded in the Mediterranean marine caves, most are regular mesolithial visitors and switchers between mesolithion and open water (53.8%), followed by accidental visitors in the mesolithion (27.3%), exclusive permanent mesolithial residents (13.6%) and mesolithial permanent residents whose populations also occur in other habitats (5.3%). Most of these species were recorded at the entrance and semidark zones of marine caves while only a small number of larger or hyperbenthic fish species, as well as of small epibenthic and cryptobenthic fishes, occur in the innermost dark sections.

6. Future Research Directions

Many questions remain unanswered concerning the diversity, spatial and ecological patterns of fishes in marine caves of the world’s oceans, due to the fragmented nature and scarcity of available data on the global scale. This study constitutes a first effort to describe general patterns and map gaps of knowledge, based on available information, with the goal of stimulating future research regarding marine cave fishes. It is not known whether the patterns observed in Mediterranean marine caves in terms of species richness and ecological habits are similar to those in under-studied marine areas. For example, is species richness in caves of other marine areas as high as that in Mediterranean caves? What are the differences between the different ecological cave zones and micro-habitats within non-Mediterranean caves? Are exclusive fish residents present in non-Mediterranean caves, and if yes, do they show adaptations similar to those living in the Mediterranean mesolithial habitats?

In situ collection of fish samples and data from marine caves relies on SCUBA diving, which involves several challenges under low-light and space-limited conditions. Multiple dives by skilled ichthyologists, marine biologists and natural history experts, are required even in the same cave in order to record highly mobile taxa and cryptobenthic species, especially those dwelling in “cave within cave” niches. However, in the absence of data, any observation has merit, and data sharing between scientists and citizens in different online platforms and biodiversity databases about fishes and marine cave environments is highly encouraged [23,163].

Even in the relatively well-studied Mediterranean marine caves, there are still important gaps in knowledge from under-studied areas (e.g., North African coasts), depth zones (e.g., mesophotic and deep-sea caves), ecological groups (e.g., cryptobenthic taxa) or about ecosystem structure, functioning and dynamics [9]. Biology and ecology of individual fishes in mesolithial habitats is largely unknown, with existing studies devoted to a single species, namely the cardinal fish *A. imberbis* [70]. The role of highly mobile larger fauna such as fishes in the trophic structure and trophodynamics of cave communities and their role in the energy flow in the caves was investigated only recently and, again, only for *A. imberbis* [121]. The potential effects of non-indigenous fishes on the marine cave biota and the functioning of cave ecosystems also remain unknown [82]. Only a few quantitative studies on fish assemblages have been published so far, and their relationship with environmental gradients are still poorly understood. In addition, anatomical, physiological and behavioural adaptations of mesolithial exclusive permanent residents have not yet been studied.

The increasing attention to marine cave environments, as shown by the increasing number of studies about marine cave fishes since the beginning of this century, gives rise to hope that these questions will be investigated in the near future.

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References

1. Proudlove, G.S. *Subterranean Fishes of the World. An Account of the Subterranean (Hypogean) Fishes Described Up to 2003 with a Bibliography 1541–2004*; International Society for Subterranean Biology: Moulis, France, 2006; p. 300.
2. Romero, A. (Ed.) The biology of hypogean fishes. In *Environmental Biology of Fishes*; Kluwer Academic Publishers: Amsterdam, The Netherlands, 2001; Volume 62, pp. 1–364.
3. Soares, D.; Niemiller, M.L. Sensory Adaptations of Fishes to Subterranean Environments. *BioScience* **2013**, *63*, 274–283. [[CrossRef](#)]
4. Illife, T.M. Biodiversity in anchialine caves. In *Encyclopedia of Caves*; Culver, D.C., White, W.B., Eds.; Elsevier Academic Press: San Diego, CA, USA, 2005; pp. 24–30.
5. Illife, T.M.; Bishop, R.E. Adaptations to life in marine caves. In *Fisheries and Aquaculture, Encyclopedia of Life Support Systems (EOLSS)*; Safran, P., Ed.; UNESCO: Paris, France; Eolss Publishers: Oxford, UK, 2007; pp. 1–27.
6. Keith, D.A.; Ferrer-Pari, J.R.; Nicholson, E.; Bishop, M.J.; Polidoro, B.A.; Ramirez-Llodra, E.; Tozer, M.G.; Nel, J.L.; Mac Nally, R.; Gregr, E.J.; et al. A function-based typology for Earth's ecosystems. *Nature* **2022**, *610*, 513–518. [[CrossRef](#)] [[PubMed](#)]
7. Gerovasileiou, V.; Illife, T.M.; Gonzalez, B.; Brankovits, D.; Martínez, A.; Keith, D.A. SM1.3 Sea caves. In *The IUCN Global Ecosystem Typology 2.0: Descriptive Profiles for Biomes and Ecosystem Functional Groups*; Keith, D.A., Ferrer-Paris, J.R., Nicholson, E., Kingsford, R.T., Eds.; IUCN: Gland, Switzerland, 2020; p. 93.
8. Surić, M.; Lončarić, R.; Lončarić, N. Submerged caves of Croatia: Distribution, classification and origin. *Environ. Earth. Sci.* **2010**, *61*, 1473–1480. [[CrossRef](#)]
9. Gerovasileiou, V.; Bianchi, C.N. Mediterranean marine caves: A synthesis of current knowledge. *Oceanogr. Mar. Biol.* **2021**, *59*, 1–88.
10. Cattaneo-Vietti, R.; Mojetta, A. The essential role of diving in Marine Biology. *BELS* **2021**, *3*, 1–44.
11. Gerovasileiou, V.; Voultziadou, E. Marine caves of the Mediterranean Sea: A sponge biodiversity reservoir within a biodiversity hotspot. *PLoS ONE* **2012**, *7*, e39873. [[CrossRef](#)]
12. Abel, E.F. Zur Kenntnis der Beziehungen der Fische zu Höhlen im Mittelmeer. *Pubbl. Staz. Zool. Napoli* **1959**, *30*, 519–528.
13. Riedl, R. *Biologie der Meereshöhlen*; Paul Parey: Hamburg, Germany; Berlin, Germany, 1966; p. 636.
14. Zander, C.D. Benthic fishes of sea caves as components of the mesolithion in the Mediterranean Sea. *Mem. Biospéol.* **1990**, *17*, 17–54.

15. Zander, C.D. Marine cave habitats. In *Encyclopedia of Caves and Karst Science*; Gunn, J., Ed.; Fitzroy Dearborn: New York, NY, USA, 2004; pp. 1072–1075.
16. Proudlove, G.S. Subterranean Fishes of the World. An Account of the Subterranean (Hypogean) Fishes with a Bibliography from 1436. Available online: <https://cavefishes.org.uk/non-stygobitic-fishes.php> (accessed on 28 February 2024).
17. Bussotti, S.; Di Franco, A.; Francour, P.; Guidetti, P. Fish assemblages of Mediterranean marine caves. *PLoS ONE* **2015**, *10*, e0122632. [[CrossRef](#)]
18. Kovačić, M.; Glavičić, I.; Paliska, D.; Valić, Z. A first qualitative and quantitative study of marine cave fish assemblages of intracave cavities. *Estuar. Coast. Shelf Sci.* **2021**, *263*, 107624. [[CrossRef](#)]
19. Ragkousis, M.; Digenis, M.; Kovačić, M.; Katsanevakis, S.; Gerovasileiou, V. Rarely reported cryptobenthic fish in marine caves of the Eastern Mediterranean Sea. *J. Mar. Sci. Eng.* **2021**, *9*, 557. [[CrossRef](#)]
20. Fricke, R.; Eschmeyer, W.N.; Van der Laan, R. (Eds.) Eschmeyer's Catalog of Fishes: Genera, Species, References. Available online: <http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp> (accessed on 28 February 2024).
21. Klimchouk, A. Caves. In *Encyclopedia of Caves and Karst Science*; Gunn, J., Ed.; Fitzroy Dearborn: New York, NY, USA, 2004; pp. 417–420.
22. Romero, A. *Cave Biology: Life in Darkness*; Cambridge University Press: New York, NY, USA, 2009; p. 306.
23. Gerovasileiou, V.; Martínez, A.; Álvarez, F.; Boxshall, G.; Humphreys, W.; Jaume, D.; Becking, L.; Muricy, G.; van Hengstum, P.; Dekeyser, S.; et al. World Register of marine Cave Species (WoRCS): A new thematic species database for marine and anchialine cave biodiversity. *Res. Ideas Outcomes* **2016**, *2*, e10451. [[CrossRef](#)]
24. Iliffe, T.M.; Kornicker, L.S. Worldwide Diving Discoveries of Living Fossil Animals from the Depths of Anchialine and Marine Caves. In *Proceedings of the Smithsonian Marine Science Symposium*; Lang, M.A., Macintyre, I.G., Rützler, K., Eds.; Smithsonian Institution Scholarly Press: Washington, DC, USA, 2009; pp. 269–280.
25. Bunnell, D. Littoral caves. In *Encyclopedia of Caves and Karst Science*; Gunn, J., Ed.; Fitzroy Dearborn: New York, NY, USA, 2004; pp. 1050–1054.
26. Mylroie, J.E. Coastal caves. In *Encyclopedia of Caves*; Culver, D.C., White, W.B., Eds.; Elsevier Academic Press: San Diego, CA, USA, 2005; pp. 122–127.
27. Sket, B. The ecology of anchialine caves. *Tree* **1996**, *11*, 221–225.
28. Iliffe, T.M.; Brankovits, D.; Gerovasileiou, V.; Gonzalez, B.; Martínez, A.; Keith, D.A. SM1.1 Anchialine caves. In *The IUCN Global Ecosystem Typology 2.0: Descriptive Profiles for Biomes and Ecosystem Functional Groups*; Keith, D.A., Ferrer-Paris, J.R., Nicholson, E., Kingsford, R.T., Eds.; IUCN: Gland, Switzerland, 2020; p. 91.
29. Sket, B. Anchialine caves. In *Encyclopedia of Caves*; Culver, D.C., White, W.B., Eds.; Elsevier Academic Press: San Diego, CA, USA, 2005; pp. 30–37.
30. Mylroie, J.E.; Carew, J.L.; Moore, A.I. Blue holes: Definition and genesis. *Carbonates Evaporites* **1995**, *10*, 225–233. [[CrossRef](#)]
31. Hissmann, K.; Fricke, H.; Schauer, J.; Ribbink, A.J.; Roberts, M.; Sink, K.; Phillip Heemstra, P. The South African coelacanth—An account of what is known after three submersible expeditions. *S. Afr. J. Sci.* **2006**, *102*, 491–500.
32. Fricke, H.; Hissmann, K.; Schauer, J.; Reinicke, O.; Kasang, L.; Plante, R. Habitat and population size of the coelacanth *Latimeria chalumnae* at Grand Comoro. *Environ. Biol. Fishes* **1991**, *32*, 287–300. [[CrossRef](#)]
33. Heemstra, P.C.; Hissmann, K.; Fricke, H.; Smale, M.J.; Schauer, J. Fishes of the deep demersal habitat at Ngazidja (Grand Comoro) Island, Western Indian Ocean. *S. Afr. J. Sci.* **2006**, *102*, 444–460.
34. Evans, J.; Aguilar, R.; Alvarez, H.; Borg, J.A.; Garcia, S.; Knittweis, L.; Schembri, P.J. Recent evidence that the deep sea around Malta is a biodiversity hotspot. *Rapp. Comm. Int. Mer Méditerran.* **2016**, *41*, 463.
35. Borg, J.A.; Evans, J.; Knittweis, L.; Schembri, P.J. *Report on the Third Analysis following the Second Surveying Phase Carried Out through Action A3. LIFE BaHAR for N2K (LIFE12 NAT/MT/000845)*; University of Malta: Valletta, Malta, 2017; p. 72.
36. List of Longest Caves. Available online: https://en.wikipedia.org/wiki/List_of_longest_caves (accessed on 28 February 2024).
37. Guinness World Records. Available online: <https://www.guinnessworldrecords.com/world-records/114059-longest-sea-cave> (accessed on 28 February 2024).
38. Zander, C.D. Fish from the mesolithial of the Red Sea. *Bull. Fish Biol.* **2018**, *17*, 1–11.
39. Laborel, J.; Vacelet, J. Étude des peuplements d'une grotte sous-marine du Golfe de Marseille. *Bull. Inst. Océan. Monaco* **1958**, *1120*, 1–20.
40. Ledoyer, M. Note sur la faune vagile des grottes sous-marines obscures. *Rapp. Comm. Int. Mer Médit.* **1965**, *18*, 121–124.
41. Ledoyer, M. Écologie de la faune vagile des biotopes méditerranéens accessibles en scaphandre autonome. I—Introduction: Données analytiques sur les biotopes de substrat dur. *Rec. Trav. Sta. Mar. Endoume* **1966**, *40*, 103–149.
42. Bath, H. *Gammogobius steinitzi* n. gen. n. sp. aus dem westlichen Mittelmeer (Pisces: Gobioidi: Gobiidae). *Senck. Biol.* **1971**, *52*, 201–210.
43. Zander, C.D.; Jelinek, H. Zur demersen Fischfauna im Bereich der Grotte von Banjole (Rovinj/YU) mit Beschreibung von *Speleogobius trigloides* n. gen. n. sp. (Gobiidae, Perciformes). *Mitt. Hamb. Zool. Mus. Inst.* **1976**, *73*, 265–280.
44. Golani, D.; Diamant, A. Biology of the sweeper, *Pempheris vanicolensis* Cuvier & Valenciennes, a Lessepsian migrant in the eastern Mediterranean, with a comparison with the original Red Sea population. *J. Fish Biol.* **1991**, *38*, 819–827.
45. Zander, C.D.; Heymer, A. Morphologische und ökologische Untersuchungen an den speleophilen Schleimfischartigen *Tripterygion melanurus* Guichenot, 1850 und *T. minor* Kolombatović, 1892 (Perciformes, Blennioidei, Tripterygiidae). *Z. Zool. Syst. Evolut.-Forsch.* **1976**, *14*, 41–59.

46. Zander, C.D.; Heymer, A. Analysis of ecological equivalents among littoral fish. In *Biology of benthic organisms, 11th European Symposium on Marine Biology, Galway, October 1976*; Keegan, B.F., Ceidigh, P.O., Boaden, P.J.S., Eds.; Pergamon Press: Oxford, UK, 1977; pp. 621–630.
47. Bibiloni, M.A.; Gili, J.M. Primera aportación al estudio de las cuevas submarinas de la isla de Mallorca. *Oecol. Aquat.* **1982**, *6*, 227–234.
48. Bori, C.; Gili, J.M.; Garcia, A. Presencia de *Oligopus ater* Risso, 1810 (Pisces, Ophidiiformes) en cuevas submarinas del litoral NE de Mallorca. *Misc. Zool.* **1985**, *9*, 401–404.
49. Harmelin, J.G.; Vacelet, J.; Vasseur, P. Les grottes sous-marines obscures: Un milieu extrême et un remarquable biotope refuge. *Téthys* **1985**, *11*, 214–229.
50. Bianchi, C.N.; Cevasco, M.G.; Diviacco, G.; Morri, C. Primi risultati di una ricerca ecologica sulla grotta marina di Bergeggi (Savona). *Boll. Mus. Ist. Biol. Univ. Genova* **1986**, *52*, 267–293.
51. Ahnelt, H.; Patzner, R.A. A new species of *Didogobius* (Teleostei: Gobiidae) from the western Mediterranean. *Cybium* **1995**, *19*, 95–102.
52. Herler, J.; Patzner, R.A.; Ahnelt, H.; Hilgers, H. Habitat selection and ecology of two speleophilic gobiid fishes (Pisces: Gobiidae) from the Western Mediterranean Sea. *PSZN Mar. Ecol.* **1999**, *20*, 49–62. [[CrossRef](#)]
53. Scsepka, S.; Ahnelt, H. Wiederbeschreibung von *Gammogobius steinitzi* Bath 1971 sowie ein Erstnachweis von *Corcyrogobius liechtensteini* (Kolombatovic 1891) für Frankreich. *Senck. Biol.* **1999**, *79*, 71–81.
54. Ahnelt, H.; Patzner, R.A. Kryptobenthische Meergrundeln von den Balearen (Westliches Mittelmeer) mit Anmerkungen zum Unterartstatus von *Chromogobius zebratus levanticus*. *Ann. Nat. Hist. Mus. Wien* **1996**, *98B*, 529–544.
55. Sartoreto, S.; Francour, P.; Harmelin, J.-H.; Charbonel, E. Observations in situ de deux Labridae profonds, *Lappanella fasciata* (Cocco, 1833) et *Acantholabrus palloni* (Risso, 1810), en Méditerranée nord-occidentale. *Cybium* **1997**, *21*, 37–44.
56. Ahnelt, H.; Herler, J.; Scsepka, S.; Patzner, R.A. First records of two rare Mediterranean Gobiidae in the northern Tyrrhenian Sea. *Cybium* **1998**, *22*, 183–186.
57. Kovačić, M. *Gammogobius steinitzi* Bath, 1971, a fish new to the Adriatic Sea. *Nat. Croat.* **1999**, *6*, 1–7.
58. Stefanni, S. A new record of *Didogobius splechnai* Ahnelt & Patzner, 1995 (Gobiidae) from the central Mediterranean Sea. *Cybium* **1999**, *23*, 105–107.
59. Bilecenoglu, M.; Taskavak, E. Some observations on the habitat of the Red Sea immigrant sweeper, *Pempheris vanicolensis*, on the Mediterranean coast of Turkey. *Zool. Middle East* **1999**, *17*, 67–70. [[CrossRef](#)]
60. Kovačić, M. Cryptobenthic gobies and clingfishes in the Kvarner area, Adriatic Sea. *Nat. Croat.* **1997**, *6*, 423–435.
61. Patzner, R.A. Habitat utilization and depth distribution of small cryptobenthic fishes (Blenniidae, Gobiidae, Gobiidae, Tripterygiidae) in Ibiza (western Mediterranean Sea). *Environ. Biol. Fishes* **1999**, *55*, 207–214. [[CrossRef](#)]
62. Arko-Pijevac, M.; Benac, Č.; Kovačić, M.; Kirinčić, M. A submarine cave at the Island of Krk (North Adriatic Sea). *Nat. Croat.* **2001**, *10*, 163–184.
63. Bussotti, S.; Denitto, F.; Guidetti, P.; Belmonte, G. Fish assemblages in shallow marine caves of the Salento Peninsula (Southern-Apulia, SE Italy). *PSZN Mar. Ecol.* **2002**, *23*, 11–20. [[CrossRef](#)]
64. Bussotti, S.; Guidetti, P.; Belmonte, G. Distribution patterns of the cardinal fish, *Apogon imberbis*, in shallow marine caves in southern Apulia (SE Italy). *Ital. J. Zool.* **2003**, *70*, 153–157. [[CrossRef](#)]
65. Harmelin, J.-G.; Boury-Esnault, N.; Fichez, R.; Vacelet, J.; Zibrowius, H. Peuplement de la grotte sous-marine de l'île de Bagaud (Parc national de Port-Cros, France, Méditerranée). *Trav. Scient. Parc Nat. Port-Cros* **2003**, *19*, 117–134.
66. Belmonte, G.; Costantini, A.; Moscatello, S.; Denitto, F.; Shkurtaj, B. Le grotte sommersa della penisola del Karaburun (Albania): Primi dati. *Thalass. Salentina* **2006**, *29*, 15–28.
67. Oertel, A.; Patzner, R.A. The biology and ecology of a submarine cave: The Grotta del Bel Torrente (Central-East Sardegna, Italy). *Mar. Ecol.* **2007**, *28*, 60–65. [[CrossRef](#)]
68. Bussotti, S.; Guidetti, P. Do Mediterranean fish assemblages associated with marine caves and rocky cliffs differ? *Estuar. Coast. Shelf Sci.* **2009**, *81*, 65–73. [[CrossRef](#)]
69. Bussotti, S.; Guidetti, P. Fish fauna of marine caves in four Italian marine protected areas. *Biol. Mar. Mediterr.* **2010**, *17*, 318–319.
70. Bussotti, S.; Di Franco, A.; Pey, A.; Vieux-Ingrassia, J.-V.; Planes, S.; Guidetti, P. Distribution patterns of marine cave fishes and the potential role of the cardinal fish *Apogon imberbis* (Linnaeus, 1758) for cave ecosystem functioning in the western Mediterranean. *Aquat. Living Resour.* **2017**, *30*, 15. [[CrossRef](#)]
71. Gerovasileiou, V.; Chintiroglou, C.; Vafidis, D.; Koutsoubas, D.; Sini, M.; Dailianis, T.; Issaris, Y.; Akritopoulou, E.; Dimarchopoulou, D.; Voultziadou, E. Census of biodiversity in marine caves of the Eastern Mediterranean Sea. *Med. Mar. Sci.* **2015**, *16*, 245–265. [[CrossRef](#)]
72. Radolović, M.; Bakran-Petricioli, T.; Petricioli, D.; Surić, M.; Perica, D. Biological response to geochemical and hydrological processes in a shallow submarine cave. *Medit. Mar. Sci.* **2015**, *16*, 305–324. [[CrossRef](#)]
73. Gerovasileiou, V.; Ganias, K.; Dailianis, T.; Voultziadou, E. Occurrence of some rarely reported fish species in eastern Mediterranean marine caves. *Cah. Biol. Mar.* **2015**, *56*, 381–387.
74. Madonna, A.; Alwany, M.A.; Rabbito, D.; Trocchia, S.; Labar, S.; Abdel-Gawad, F.K.; D'Angelo, R.; Gallo, A.; Guerriero, G.; Ciarcia, G. Caves biodiversity in the marine area of Riviera d'Ulisse Regional Park, Italy: Grotta del Maresciallo overview. *J. Biodivers. Endanger. Species* **2015**, *3*, 1000153. [[CrossRef](#)]
75. Jimenez, C.; Achilleos, K.; Petrou, A.; Hadjioannou, L.; Guido, A.; Rosso, A.; Gerovasileiou, V.; Albano, P.G.; Di Franco, D.; Andreou, V.; et al. A dream within a dream: Kakoskali Cave, a unique marine ecosystem in Cyprus (Levantine Sea). In *Marine Caves of the Eastern Mediterranean Sea. Biodiversity, Threats and Conservation*; Turkish Marine Research Foundation (TUDAV) Publication No: 53; Öztürk, B., Ed.; TUDAV: Istanbul, Turkey, 2019; pp. 91–110.

76. Mačić, V.; Panou, A.; Bundone, L.; Varda, D.; Pavičević, M. First inventory of the semi-submerged marine caves in South Dinarides karst (Adriatic coast) and preliminary list of species. *Turk. J. Fish. Aquat. Sci.* **2019**, *19*, 765–774. [[CrossRef](#)]
77. Bilecenoglu, M. Diversity of cavern fishes at the Eastern Aegean Sea coasts (Turkey): Preliminary observation. In *Marine Caves of the Eastern Mediterranean Sea. Biodiversity, Threats and Conservation*; Turkish Marine Research Foundation (TUDAV) Publication No: 53; Öztürk, B., Ed.; TUDAV: Istanbul, Turkey, 2019; pp. 84–90.
78. Çelikok, M. Marine caves alongside Fethiye/Turkey coasts. In *Marine Caves of the Eastern Mediterranean Sea. Biodiversity, Threats and Conservation*; Turkish Marine Research Foundation (TUDAV) Publication No: 53; Öztürk, B., Ed.; TUDAV: Istanbul, Turkey, 2019; pp. 111–125.
79. Turan, C.; Uygur, N.; İğde, M.; Doğdu, S.A. Habitat mapping of underwater Bilge Taş Cave (Wisdom Stone Cave) in the Northeastern Mediterranean Sea: Structure and biodiversity. In *Marine Caves of the Eastern Mediterranean Sea. Biodiversity, Threats and Conservation*; Turkish Marine Research Foundation (TUDAV) Publication No: 53; Öztürk, B., Ed.; TUDAV: Istanbul, Turkey, 2019; pp. 195–206.
80. Galil, B.S.; Goren, M. Rosh-Hanikra Grottoes, Israel—A refuge for the critically endangered and for opportunistic invasives. In *Marine Caves of the Eastern Mediterranean Sea. Biodiversity, Threats and Conservation*; Turkish Marine Research Foundation (TUDAV) Publication No: 53; Öztürk, B., Ed.; TUDAV: Istanbul, Turkey, 2019; pp. 159–165.
81. Gerovasileiou, V.; Voultziadou, E.; Issaris, Y.; Zenetos, A. Alien biodiversity in Mediterranean marine caves. *Mar. Ecol.* **2016**, *37*, 239–256. [[CrossRef](#)]
82. Gerovasileiou, V.; Bancila, R.I.; Katsanevakis, S.; Zenetos, A. Introduced species in Mediterranean marine caves: An increasing but neglected threat. *Mediterr. Mar. Sci.* **2022**, *23*, 995–1005. [[CrossRef](#)]
83. Nielsen, J.G.; Cohen, D.M. *Grammonus thieiei* (Ophidiiformes: Bythitidae): A new bythitid cavefish from off Sulawesi, Indonesia. *Beagle* **2004**, *20*, 83–86. [[CrossRef](#)]
84. Nielsen, J.G. *Grammonus yunokawai* (Ophidiiformes: Bythitidae), a new marine cavefish from the Ryukyu Islands. *Ichthyol. Res.* **2007**, *54*, 374–379. [[CrossRef](#)]
85. Hagiwara, K.; Winterbottom, R. Two new species of *Trimma* (Gobiidae) from the Western Pacific. *Bull. Natl. Mus. Nat. Sci. Ser. A* **2007**, *Supplement No. 1*, 163–174.
86. Gill, A.C.; Tea, Y.-K.; Senou, H. *Pseudanthias tequila*, a new species of anthiadine serranid from the Ogasawara and Mariana Islands. *Zootaxa* **2017**, *4341*, 67–76. [[CrossRef](#)] [[PubMed](#)]
87. Lam, K.; Leung, A.W.Y.; Morton, B.; Hodgson, P. A checklist of fish species identified from Conic Island Cave, Hong Kong. *J. Nat. Hist.* **2008**, *42*, 967–970. [[CrossRef](#)]
88. Randall, J.E.; Hughes, M.J. *Grammonus nagaredai*, a new viviparous marine fish (Ophidiiformes: Bythitidae) from the Hawaiian Islands. *Pac. Sci.* **2008**, *63*, 137–146. [[CrossRef](#)]
89. Johnson, G.D.; Ida, H.; Sakaue, J.; Sado, T.; Asahida, T.; Miya, M. A ‘living fossil’ eel (Anguilliformes: Protanguillidae, fam. nov.) from an undersea cave in Palau. *Proc. Biol. Sci.* **2012**, *279*, 934–943. [[CrossRef](#)] [[PubMed](#)]
90. Hui, T.H.; Naruse, T.; Fujita, Y.; Kiat, T.S. Observations on the fauna from submarine and associated anchialine caves in Christmas Island, Indian Ocean Territory. *Raffles Bull. Zool. Suppl.* **2014**, *30*, 406–418.
91. Allen, G.R.; Walsh, F. *Plectranthias bennetti*, a new species of anthiine fish (Pisces: Serranidae) from the Coral Sea, Australia. *J. Ocean Sci. Found.* **2015**, *16*, 82–89.
92. Greenfield, D.W.; Randall, J.E. *Eviota lentiginosa*, a new dwarfgoby from Norfolk Island, Australia (Teleostei: Gobiidae). *J. Ocean Sci. Found.* **2017**, *29*, 66–71.
93. Ngai, D.N.; Thao, D.V.; Thung, D.C.; Thuy, L.Z.; Tien, D.D.; Vquan, N.; Chien, P.V. Biological community in submerged caves and marine lakes in Ha Long-Cat Ba Area, Vietnam. *J. Life Sci.* **2015**, *9*, 541–548.
94. Allen, G.R.; Erdmann, M.V.; Mahardini, A. *Cercamia melanogaster*, a new species of cardinalfish (Apogonidae) from West Papua, Indonesia. *J. Ocean Sci. Found.* **2015**, *14*, 57–65.
95. Lubbock, R. Fishes of the family Pseudochromidae (Perciformes) in the northwest Indian Ocean and Red Sea. *J. Zool.* **1975**, *176*, 115–157. [[CrossRef](#)]
96. Winterbottom, R.; Bogorodsky, S.V.; Alpermann, T.J. A new species of *Trimma* of the *T. taylori* species group (Teleostei: Gobiidae) from the Red Sea, Indian Ocean. *Zootaxa* **2023**, *5353*, 250–264.
97. Micael, J.; Azevedo, J.M.N.; Costa, A.C. Biological characterisation of a subtidal tunnel in São Miguel island (Azores). *Biodivers. Conserv.* **2006**, *15*, 3675–3684. [[CrossRef](#)]
98. Cullity, K. Species diversity among marine caves in Bermuda. *J. Mar. Ecol.* **2012**, *1*, 83–90.
99. Kovtun, O.; Manilo, L. Mediterranean fish—*Gammogobius steinitzi* Bath, 1971 (Actinopterygii: Perciformes: Gobiidae)—A new representative of the Black Sea ichthyofauna. *Acta Ichthyol. Piscat.* **2013**, *43*, 307–314. [[CrossRef](#)]
100. Ereskovsky, A.V.; Kovtun, O.A.; Pronin, K.K. Marine cave biota of the Tarkhankut Peninsula (Black Sea, Crimea), with emphasis on sponge taxonomic composition, spatial distribution and ecological particularities. *J. Mar. Biol. Assoc. UK* **2016**, *96*, 391–406. [[CrossRef](#)]
101. Møller, P.R.; Schwarzhans, W.; Iliffe, T.M.; Nielsen, J. Revision of the Bahamian cave-fishes of the genus *Lucifuga* (Ophidiiformes, Bythitidae), with description of a new species from islands on the Little Bahama Bank. *Zootaxa* **2006**, *1223*, 23–46. [[CrossRef](#)]
102. Williams, J.T.; Delrieu-Trottin, E.; Planes, S. Two new fish species of the subfamily Anthiinae (Perciformes, Serranidae) from the Marquesas. *Zootaxa* **2013**, *3647*, 167–180. [[CrossRef](#)]

103. Muricy, G.; Lage, A.; Sandes, J.; Klautau, M.; Pinheiro, U.; Laport, M.S.; de Oliveira, B.F.R.; Pequeno, C.B.; Lopes, M.V. Sponge communities of submarine caves and tunnels on the Fernando de Noronha Archipelago, Northeast Brazil. *J. Mar. Sci. Eng.* **2024**, *12*, 657. [[CrossRef](#)]
104. Depczynski, M.; Bellwood, D.R. Microhabitat utilisation patterns in cryptobenthic coral reef fish communities. *Mar. Biol.* **2004**, *145*, 455–463. [[CrossRef](#)]
105. Trajano, E. Ecological classification of subterranean organisms. In *Encyclopedia of Caves*, 2nd ed.; White, W.B., Culver, D.C., Eds.; Academic Press: Waltham, MA, USA, 2012; pp. 230–234.
106. Trajano, E.; Carvalho, M.R. Towards a biologically meaningful classification of subterranean organisms: A critical analysis of the Schiner-Racovitza system from a historical perspective, difficulties of its application and implications for conservation. *Subterr. Biol.* **2017**, *22*, 1–26. [[CrossRef](#)]
107. Dulčić, J.; Kovačić, M. *Ihtiofauna Jadranskog Mora*; Golden marketing—Tehnička knjiga and Institute for oceanography and Fishery: Zagreb, Croatia; Split, Croatia, 2020; p. 677.
108. Kovačić, M. Hyperbenthic gobies in the Kvarner area, Adriatic Sea. *J. Fish Biol.* **2003**, *63*, 1051–1055. [[CrossRef](#)]
109. Kovačić, M.; Patzner, R.A.; Schliewen, U.K. A first quantitative assessment of the ecology of cryptobenthic fishes in the Mediterranean Sea. *Mar. Biol.* **2012**, *159*, 2731–2742. [[CrossRef](#)]
110. Friedman, S.T.; Price, S.A.; Corn, K.A.; Larouche, O.; Martinez, C.M.; Wainwright, P.C. Body shape diversification along the benthic–pelagic axis in marine fishes. *Proc. R. Soc. B* **2020**, *287*, 20201053. [[CrossRef](#)] [[PubMed](#)]
111. FishBase. *World Wide Web Electronic Publication*; Froese, R., Pauly, D., Eds.; 2024; Available online: <https://www.fishbase.org> (accessed on 28 February 2024).
112. Glavičić, I.; Kovačić, M.; Soldo, A.; Schliewen, U. A quantitative assessment of the diel influence on the cryptobenthic fish assemblage of the shallow Mediterranean infralittoral zone. *Sci. Mar.* **2020**, *84*, 49–57. [[CrossRef](#)]
113. Wagner, M.; Kovačić, M.; Koblmüller, S. Unravelling the taxonomy of an interstitial fish radiation: Three new species of *Gouania* (Teleostei: Gobiidae) from the Mediterranean Sea and redescrptions of *G. willdenowi* and *G. pigra*. *J. Fish Biol.* **2020**, *98*, 64–88. [[CrossRef](#)] [[PubMed](#)]
114. Vukić, J.; Bilá, K.B.; Soukupová, T.; Kovačić, M.; Šanda, R.; Kratochvíl, L. Convergent evolution in shape in European gobies. *Evolution* **2024**, submitted.
115. Gerovasileiou, V.; Akel, E.H.K.; Akyol, O.; Alongi, G.; Azevedo, F.; Babali, N.; Bakiu, R.; Bariche, M.; Bennoui, A.; Castriota, L.; et al. New Mediterranean Biodiversity Records (July, 2017). *Mediterr. Mar. Sci.* **2017**, *18*, 355–384.
116. Digenis, M.; Akyol, O.; Benoit, L.; Biel-Cabanelas, M.; Çamlık, Ö.; Charalampous, K.; Chatzistryrou, A.; Crocetta, F.; Deval, M.; Di Capua, I.; et al. New records of rarely reported species in the Mediterranean Sea (March 2024). *Mediterr. Mar. Sci.* **2024**, *25*, 84–115. [[CrossRef](#)]
117. Nelson, J.S.; Grande, T.C.; Wilson, M.V.H. *Fishes of the World*, 5th ed.; John Wiley & Sons: Hoboken, NJ, USA, 2016; p. 707.
118. Proudlove, G.; Medina-González, R.; Chumba-Segurab, L.; Iliffe, T. Threatened fishes of the world: *Ogilbia pearsei* (Hubbs, 1938) (Bythitidae). *Environ. Biol. Fishes* **2001**, *62*, 214. [[CrossRef](#)]
119. Poulson, T.L. Adaptations of cave fishes with some comparisons to deep-sea fishes. *Environ. Biol. Fishes* **2001**, *62*, 345–364. [[CrossRef](#)]
120. Anderson, W.D., Jr.; Johnson, G.D.; Baldwin, C.C. Review of the splendid perches, *Callanthias* (Percoidei: Callanthiidae). *Trans. Am. Philos. Soc.* **2015**, *105*, 1–126.
121. Bussotti, S.; Di Franco, A.; Bianchi, C.N.; Chevaldonné, P.; Egea, L.; Fanelli, E.; Lejeusne, C.; Musco, L.; Navarro-Barranco, C.; Pey, A.; et al. Fish mitigate trophic depletion in marine cave ecosystems. *Sci. Rep.* **2018**, *8*, 9193. [[CrossRef](#)] [[PubMed](#)]
122. Erguden, D.; Uygur, N.; Erguden, S.A. First occurrence of juvenile *Sargocentron rubrum* (Forsskal, 1775) from South-Eastern Mediterranean, Turkey. *Mar. Fish. Sci.* **2023**, *36*, 203–208. [[CrossRef](#)]
123. Randall, J.E. Revision of the Indo-Pacific Labrid Fish Genus *Wetmorella*. *Copeia* **1983**, *1983*, 875–883. [[CrossRef](#)]
124. Fernandez-Silva, I.; Ho, H.-C. Revision of the circumtropical glass-eye fish *Heteropriacanthus cruentatus* (Perciformes: Priacanthidae), with resurrection of two species. *Zootaxa* **2017**, *4273*, 341–361. [[CrossRef](#)] [[PubMed](#)]
125. Nair, R.J.; Dineshkumar, S. New distributional records of three soldier fishes (Pisces: Holocentridae: Myripristis) from Indian waters. *Mar. Biodiv. Rec.* **2016**, *9*, 89. [[CrossRef](#)]
126. Herler, J.; Patzner, R.A. Spatial segregation of two common *Gobius* species (Teleostei: Gobiidae) in the northern Adriatic Sea. *Mar. Ecol.* **2005**, *26*, 121–129. [[CrossRef](#)]
127. Glavičić, I.; Paliska, D.; Soldo, A.; Kovačić, M. A quantitative assessment of the cryptobenthic fish assemblage at deep littoral cliffs in the Mediterranean. *Sci. Mar.* **2016**, *80*, 329–337.
128. Kotrschal, K. Northern Adriatic rocky reef fishes at low winter temperatures. *PSZN Mar. Ecol.* **1983**, *4*, 275–286. [[CrossRef](#)]
129. Kotrschal, K.; Reynolds, W.W. Behavioural ecology of Northern Adriatic reef fishes in relation to seasonal temperature regimes. *Contr. Mar. Sc.* **1982**, *25*, 99–106.
130. Harmelin, J.-G. Structure et variabilité de l'ichtyofaune d'une zone rocheuse protégée en Méditerranée (Parc national de Port-Cros, France). *Mar. Ecol.* **1987**, *8*, 263–284. [[CrossRef](#)]
131. Azzurro, E.; Pais, A.; Consoli, P.; Andaloro, F. Evaluating day–night changes in shallow Mediterranean rocky reef fish assemblages by visual census. *Mar. Biol.* **2007**, *151*, 2245–2253. [[CrossRef](#)]

132. Nieder, J.; Zander, C.D. Nocturnal activity of a blenny *Lipophrys trigloides* (Pisces, Blenniidae) at the Spanish Mediterranean coast. *Misc. Zool.* **1993–1994**, *17*, 189–197.
133. Kovačić, M.; Lipej, L.; Dulčić, J.; Iglesias, S.; Goren, M. Evidence-based checklist of the Mediterranean Sea fishes. *Zootaxa* **2021**, *4998*, 1–115. [[CrossRef](#)] [[PubMed](#)]
134. Miller, P.J. Gobiidae. In *Fishes of the North-Eastern Atlantic and the Mediterranean, Vol II*; Whitehead, P.J.P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J., Tortonese, E., Eds.; UNESCO: Paris, France, 1986; pp. 1019–1085.
135. Kotschal, K. Blennies and endolithic bivalves: Differential utilization of shelter in Adriatic Blenniidae (Pisces: Teleostei). *PSZN Mar. Ecol.* **1988**, *9*, 253–269. [[CrossRef](#)]
136. Digenis, M.; Arvanitidis, C.; Dailianis, T.; Gerovasileiou, V. Comparative study of marine cave communities in a protected area of the South-Eastern Aegean Sea, Greece. *J. Mar. Sci. Eng.* **2022**, *10*, 660. [[CrossRef](#)]
137. Lipej, L.; Kovačić, M.; Dulčić, J. An analysis of Adriatic ichthyofauna—Ecology, zoogeography, and conservation status. *Fishes* **2022**, *7*, 58. [[CrossRef](#)]
138. Ramos-Esplá, A.A.; Bitar, G.; Khalaf, G.; El-Shaer, H.; Forcada, A.; Limam, A.; Ocaña, O.; Sghaier, Y.R.; Valle, C. *Ecological Characterization of Sites of Interest for Conservation in Lebanon: Enfeh Peninsula, Ras Chekaa cliffs, Raoucheh, Saida, Tyre and Nakoura*. Regional Activity Centre for Specially Protected Areas (RAC/SPA); United Nations Environment Programme/Mediterranean Action Plan (UNEP/MAP), MedMPAnet Project: Tunis, Tunisia, 2014; 146p.
139. Díaz, D.; Ballesteros, E.; Cebrián, E.; Aspillaga, E.; Muñoz, A. Les coves submergides de l'arxipèlag de Cabrera. In *Arxipèlag de Cabrera: Història Natural*; Grau, A.M., Fornós, J.J., Mateu, G., Oliver, P.A., Terrasa, B., Eds.; Monografies de la Societat d'Història Natural de les Balears 30; Societat d'Història Natural de les Balears: Palma, Spain, 2020; pp. 299–316.
140. Zenetos, A.; Akel, E.; Apostolidis, C.; Bilecenoglu, M.; Bitar, G.; Buchet, V.; Chalari, N.; Corsini-Foka, M.; Crocetta, F.; Dogrammatzi, A.; et al. New Mediterranean Biodiversity Records (April 2015). *Mediterr. Mar. Sci.* **2015**, *16*, 266–284. [[CrossRef](#)]
141. Novosel, M.; Bakran-Petricioli, T.; Požar-Domac, A.; Kružić, P.; Radić, I. The benthos of the northern part of the Velebit Channel (Adriatic Sea, Croatia). *Nat. Croat.* **2002**, *11*, 387–409.
142. Onorato, R.; Denitto, F.; Belmonte, G. Le grotte costiere del Salento. Classificazione, localizzazione, descrizione. *Thalass. Sal.* **1999**, *23*, 67–116.
143. Crocetta, F.; Agius, D.; Balistreri, P.; Bariche, M.; Bayhan, Y.; Çakir, M.; Ciriaco, S.; Corsini-Foka, M.; Deidun, A.; El Zrelli, R.; et al. New Mediterranean Biodiversity Records (October 2015). *Mediterr. Mar. Sci.* **2015**, *16*, 682–702. [[CrossRef](#)]
144. Onorato, M.; Belmonte, G. Submarine caves of the Salento Peninsula: Faunal aspects. *Thalass. Sal.* **2017**, *39*, 47–72.
145. Zavodnik, D.; Pallaoro, A.; Jaklin, A.; Kovačić, M.; Arko-Pjevac, M. A benthos survey of the Senj Archipelago (North Adriatic Sea, Croatia). *Acta Adriat.* **2005**, *46*, 3–68.
146. Guidetti, P.; Causio, S.; Licchelli, C. The first record of *Enchelycore anatina* (Muraenidae: Pisces) in the Ionian Sea (Mediterranean basin). *Mar. Biodivers. Rec.* **2012**, *5*, e22. [[CrossRef](#)]
147. Öztürk, B. (Ed.) *Marine Caves of the Eastern Mediterranean Sea. Biodiversity, Threats and Conservation*; Turkish Marine Research Foundation (TUDAV) Publication No: 53; TUDAV: Istanbul, Turkey, 2019; p. 258.
148. Kovačić, M.; Miletić, M.; Papageorgiou, N. A first checklist of gobies from Crete with ten new records. *Cybium* **2011**, *35*, 245–253.
149. Uriz, M.J.; Zabala, M.; Ballesteros, E.; Garcia-Rubies, A.; Turón, X. El bentos: Les coves. In *Història Natural de l'Arxipèlag de Cabrera*; Alcover, J.A., Ballesteros, E., Fornós, J.J., Eds.; CSIC-Moll: Palma de Mallorca, Spain, 1993; pp. 731–748.
150. Ramos-Esplá, A.A.; Bitar, G.; Forcada, A.; Limam, A.; Ocaña, O.; Sghaier, Y.R.; Samaha, Z.; Valle, C. *Ecological Characterization of Potential New MPAs in Lebanon: Batroun, Medfoun and Byblos*; SPA/RAC: Tunis, Tunisia; MedMPA Network Project: Tunis, Tunisia, 2017; 87p.
151. Tsiamis, K.; Aydogan, Ö.; Bailly, N.; Balistreri, P.; Bariche, M.; Carden-Noad, S.; Corsini-Foka, M.; Crocetta, F.; Davidov, B.; Dimitriadis, C.; et al. New Mediterranean biodiversity records (July 2015). *Mediterr. Mar. Sci.* **2015**, *16*, 472–488. [[CrossRef](#)]
152. Navarro-Barranco, C. *Faunistic and Ecological Study of the Amphipods Inhabiting Submarine Caves in the Southern Iberian Peninsula*. Ph.D. Thesis, University of Seville, Seville, Spain, 2015.
153. Zander, C.D. Tripterygiidae. In *Fishes of the North-Eastern Atlantic and the Mediterranean*; Whitehead, P.J.P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J., Tortonese, E., Eds.; UNESCO: Paris, France, 1986; Volume II, pp. 1118–1121.
154. Trajano, E.; Bichuette, M.E.; Kapoor, B.G. *Biology of Subterranean Fishes*; Science Publishers: Enfield, NH, USA, 2010; p. 480.
155. Romero, A. Cave as biological spaces. *Polymath* **2012**, *2*, 1–15.
156. Nielsen, J.G.; Cohen, D.M.; Markle, D.F.; Robins, C.R. *FAO Species Catalogue, Vol. 18. Ophidiiform Fishes of the World (Order Ophidiiformes). An Annotated and Illustrated Catalogue of Pearlfishes, Cuskeels, Brotulas and Other Ophidiiform Fishes Known to Date*; FAO Fisheries Synopsis No. 125; FAO: Rome, Italy, 1999; Volume 18, p. 178.
157. Bogorodsky, S.V.; Suzuki, T.; Mal, A.O. Description of a new species of *Priolepis* (Perciformes: Gobiidae) from the Red Sea, a new record of *Priolepis compita*, and a distributional range extension of *Trimma fishelsoni*. *Zootaxa* **2016**, *4150*, 168–184. [[CrossRef](#)]
158. Delventhal, N.R.; Mooi, R.D.; Bogorodsky, S.V.; Mal, A.O. A review of the *Callogobius* (Teleostei: Gobiidae) from the Red Sea with the description of a new species. *Zootaxa* **2016**, *4179*, 225–243. [[CrossRef](#)]
159. Winterbottom, R.; Pyle, R.L. A new species of *Trimma* (Teleostei: Gobiidae) from the deep reefs of Vanuatu, western Pacific Ocean. *J. Ocean. Sci. Found.* **2022**, *39*, 2–8.
160. Tornabene, L.; Van Tassell, J.L.; Gilmore, R.G.; Robertson, D.R.; Young, F.; Baldwin, C.C. Molecular phylogeny, analysis of character evolution, and submersible collections enable a new classification of a diverse group of gobies (Teleostei: Gobiidae: Nes subgroup), including nine new species and four new genera. *Zool. J. Linn. Soc.* **2016**, *177*, 764–812. [[CrossRef](#)]

161. Kovačić, M.; Renoult, J.P.; Pillon, R.; Svensen, R.; Bogorodsky, S.V.; Engin, S.; Louisy, P. Identification of Mediterranean marine gobies (Actinopterygii: Gobiidae) of the continental shelf from photographs of in situ individuals. *Zootaxa* **2022**, *5144*, 1–103. [[CrossRef](#)]
162. Kuitert, R.; Kozawa, T. *Cardinalfishes of the World*; Aquatic Photographics & Anthis: Seaford, Australia; Okazaki, Japan, 2019; p. 198.
163. Nicolosi, G.; Gerovasileiou, V. Towards invasion ecology for subterranean ecosystems. *Biodivers. Conserv.* **2024**, *33*, 1561–1569. [[CrossRef](#)]

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