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REVIEW ARTICLE

Alien biodiversity in Mediterranean marine caves

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Abstract

The number of alien species in the Mediterranean Sea is increasing rapidly, but few attempts have been made to evaluate impacts on specific habitat types. The present study investigated alien biodiversity in Mediterranean marine caves, both by contributing new records of Eastern Mediterranean cave aliens, and by reviewing the scattered existing literature; the main goals were to highlight potential impacts and investigate the importance of cave environments for the expansion of alien species. Seven new alien species were found in marine caves of the Aegean and Ionian seas, raising the total number of aliens reported from Mediterranean marine caves to 56 species, classified as molluscs, cnidarians, bryozoans, polychaetes, crustaceans, macroalgae, fishes and tunicates. Most cave aliens (66%) were recorded from the Southeastern Levantine coasts, specifically from Lebanese caves. Shipping and Lessepsian migration have been suggested as the main pathways of alien introduction into caves of the Mediterranean Sea. The comparison of alien cave biodiversity with the updated Mediterranean alien inventory (32 species added to the latest inventory) showed similar patterns and trends for species richness, biogeographical origin and major introduction pathways, corroborating previous findings on the high local representativeness of Mediterranean cave biodiversity. Alien species seem to have invaded mostly the entrance and semi-dark zones of shallow and/or semi-submerged caves and tunnels, whereas only a few have reached the dark inner sectors or caves of the anchialine type; thus, the unfavourable cave environment seems to be naturally protected from impacts related to opportunistic invasive species, at least to a certain point. Currently there is no research confirming any direct impacts of alien biota on the native cavernicolous one. However, some issues have emerged, implying potential threats that need to be further explored: (i) the presence of a considerable proportion of aliens in most studied marine caves of the Southeastern Mediterranean basin, (ii) the recently observed population explosion of alien cave-dwelling fishes in the same area, (iii) several indications that alien diversity in marine caves is much higher than we know today. Quantitative surveys and monitoring schemes are needed in order to evaluate potential effects of alien diversity on cave community structure and the role of marine caves as stepping stones for its expansion in the Mediterranean.

Introduction

Over recent decades, the number of alien species in the Mediterranean Sea, especially in its southeastern basin, has increased continuously (Raitsos *et al.* 2010; Zenetos *et al.* 2010, 2012; Tzomos *et al.* 2012). Aliens have invaded a wide variety of habitats, from coastal waters to deeper areas.

In most cases, alien species have been recorded accidentally or in the framework of citizen science projects by recreational divers and fishermen (Zenetos *et al.* 2013; Kapiris *et al.* 2014; Katsanevakis *et al.* 2014a), by scientists during general ecological studies (Alongi *et al.* 2012) or in dedicated assessments in particular areas (Bazairi *et al.* 2013). Data on their habitat preferences are usually incorporated in faunistic papers and large biodiversity databases, or are overlooked. Until today, few attempts have been made to compile the scattered information on alien biodiversity of certain habitat types, such as coral reefs (*e.g.* Coles & Eldredge 2002) and coastal lagoons, which constitute hotspots for biological invasions (Olenin & Leppäkoski 1999; Occhipinti Ambrogi 2000; Verlaque 2001; Rilow & Galil 2009). Such information could be useful for monitoring potential impacts of biological invasions in different habitat types. This could be critical for vulnerable ecosystems that harbour unique diversity and a high number of endemic species. Additionally, relevant approaches could be interesting for predicting the future distributional range of alien species, given that favourable habitat types could function as stepping stones for further expansion.

The presence of alien species in cave environments has to date been a subject of study only for terrestrial caves. This research has shown that alien species may reach high percentages of cavernicolous diversity in certain areas, competing with endemic fauna (Reeves 1999). However, to our knowledge, no similar research has been carried out on marine caves. In the framework of a current overview of the Mediterranean marine cave biodiversity (see Gerovasileiou & Voultsiadou 2014), we noticed the presence of numerous alien species in different types and sectors of marine caves from several areas. Mediterranean marine caves have been characterized as 'refuge habitats' or 'biodiversity reservoirs' because their sciaphilic communities harbour rich diversity, including a high number of rare, endemic and archaic forms (Harmelin *et al.* 1985; Bianchi *et al.* 2012; Gerovasileiou & Voultsiadou 2012). Cave communities in the Mediterranean range from semi-sciaphilic to entirely dark, reflecting the particular topography and abiotic gradients of individual caves (Riedl 1966). They are considered ecosystems with low resilience (Harmelin *et al.* 1985), with recreational diving, water temperature rise, coastal infra-structure construction and marine pollution recognized as the main threats for cave biota (Giakoumi *et al.* 2013). Recently, in Western Mediterranean caves, increasing water temperature owing to climate change has induced replacement of cold-water species with congeneric ones exhibiting tolerance to thermal rise (Chevaldonné & Lejeusne 2003). Cave assemblages are protected by the EU Habitats Directive (92/43/EEC) and have been included in two Action Plans adopted by the contracting parties of the Barcelona Convention (UNEP-MAP-RAC/SPA 2008, 2015).

Considering the unique character of marine cave biota and the significance of cave environments for Mediterranean biodiversity, the aims of the present work were to: (i) give an overview of alien diversity in marine caves of the Mediterranean Sea; (ii) investigate potential impacts on cave communities; (iii) examine the importance of cave habitats for the expansion of alien species. To approach the latter goal, an update of the Mediterranean alien species inventory was compiled.

Material and Methods

The present study was carried out in the framework of a broader overview of Mediterranean marine cave biodiversity, which is currently underway (see Gerovasileiou & Voultsiadou 2014). Approximately 300 scientific studies, including journal articles, monographs, conference proceedings and research project reports, were collected, and cave biodiversity records were incorporated into a database (see Methods sections in Gerovasileiou & Voultsiadou 2012, 2014). All species were taxonomically updated according to the World Register of Marine Species (WoRMS Editorial Board 2014). The resulting biodiversity lists were cross-checked with recent studies on Mediterranean alien biodiversity (*e.g.* Zenetos *et al.* 2009, 2010, 2012; Gravili *et al.* 2013) and online databases (EASIN 2014; ELNAIS 2014). Research articles and monographs recording alien biodiversity (*e.g.* Galil *et al.* 2002; Golani *et al.* 2002; Zenetos *et al.* 2004; Bilecenoglu 2010) were also examined for records from marine caves. Furthermore, an update of Mediterranean alien diversity was compiled, based on the Hellenic Centre for Marine Research/European Environment Agency off-line database following the latest inventory by Zenetos *et al.* (2012). The term alien here is widely used to include also cryptogenic species (i.e. species of unknown origin).

Moreover, during the last 6 years (2009–2014), several marine caves of the Ionian, Aegean and Levantine seas were surveyed for their diversity in the framework of different research projects and alien species were sampled and/or photographed when present. Information given by recreational SCUBA divers (web fora and direct communication) was also taken into account.

For each species record, the available ecological (*i.e.* cave zone and substrate type) and spatial information was incorporated into our database. The biogeographical division of the Mediterranean Sea followed by Gerovasileiou & Voultsiadou (2012) was used for the spatial categorization of data. However, certain modifications were made according to data availability: records from the Balearic Islands and West Sardinia were merged and assigned as 'Balearic Sea' (BA).

In a first effort to examine zoogeographical patterns and potential introduction trends of alien marine cave biota, all species were assigned to the corresponding categories according to the relevant bibliographic sources (Katsanevakis *et al.* 2012; Zenetos *et al.* 2012; EASIN 2014). For regional comparisons, the aforementioned areas were grouped in four broader areas according to the Marine Strategy Framework Directive (EU 2008), as Zenetos *et al.* (2012) did for the entire Mediterranean alien diversity: (i) the Western Mediterranean (WMED), (ii) the Central Mediterranean (CMED), (iii) the Adriatic (ADRIA) and (iv) the Eastern Mediterranean (EMED).

Results and Discussion

A total of 56 alien species has been reported to date in ~50 marine caves and tunnels of the Mediterranean. Seven of these species are new records added by the present research in Aegean and Ionian marine caves. Detailed data concerning location and name of the cave, literature source, ecological zone and type of substrate, as well as impact, origin and pathway of introduction for each species are presented in Table 1. The alien marine cave biota was found to consist of five macroalgae, nine cnidarians, 15 molluscs, nine polychaetes, six crustaceans, seven bryozoans, two tunicates and three fish species. Details about their discovery and information on their ecology are given below.

Records of alien species

Macro-algae

The rapid decrease of light towards the interior of the marine cave environment usually limits the development of macro-algae at the more or less sciaphilic entrance zone. Five species of alien macro-algae have been recorded in Mediterranean marine caves to date, mainly at the entrance zone (one ochrophyte, one chlorophyte and three rhodophytes). Alongi *et al.* (2012) found that the existence of the aliens *Acrothamnion preissii*, *Asparagopsis armata* and *Caulerpa cylindracea* at the entrance of the surveyed caves of Lampedusa and Sicily did not seem to have negative effects on the native flora. *Womersleyella setacea* was also listed as an alien species in Italian marine caves in an online database (Habitat Italia 2014). *Womersleyella setacea*, along with *A. preissii* and *C. cylindracea* have been reported from Mediterranean coralligenous bottoms; the former species was considered as the most impacting alien for this community, which often forms rims at the entrance of marine caves (Ballesteros 2006). Our observations from the Aegean Sea verified that *C. cylindracea*, which often thrives in sciaphilic walls of the area (Gerovasileiou *et al.* 2009), is usually absent close to cave openings, where light levels decrease steeply. The rhodophyte *As. armata* was also recorded in the present study from numerous small semi-dark caves and overhangs in Saronikos Bay.

Cnidarians

Eight alien species of Hydrozoa have been found in Mediterranean marine caves, amongst which *Clytia linearis* seems to be the most widespread. This circumtropical species is possibly the most successful Lessepsian migrant in the Mediterranean Sea, as it has been recorded to be abundant in shallow waters and shaded rocky beds of the entire basin (Gravili *et al.* 2013). In marine caves it was first found at the entrance and semi-dark zones of Sa Catedral and Es Faralló caves in Mallorca, under the name *Clytia gravieri* (Billard 1904) by Gili & García-Rubies (1985). Since then, it has been reported from several marine caves in the Gulf of Naples, Lampedusa, Sicily, Apulia and Lebanon (Table 1). Moscatello & Belmonte (2007), who described the plankton assemblages in a semi-submerged cave of Salento Peninsula (Apulia), found meroplanktonic polyps of the species from the cave exterior to the dark internal zone, 60–90 m from the entrance. Denitto *et al.* (2007) found *C. linearis*, along with the alien species *Mitrocomium medusiferum* (under the name *Campalecium medusiferum* Torrey, 1902), settled on baked-clay panels deployed in the same cave during an experiment on larval settlement and primary succession processes.

A recent study on the hydrozoan fauna of the Levant Sea by Morri *et al.* (2009) brought to light six alien species, which mainly inhabited the entrance zone of shallow marine caves and tunnels of Lebanon. Of them, *Dynamena quadridentata* and *Sertularia tongensis* (cited under the name *Sertularella thecocarpa* Jarvis, 1922) were recorded for the first time in the Mediterranean Sea. The most frequent species (frequency expressed as occurrence of a given species with respect to the total number of samples) in the surveyed caves were *Filellum serratum* (frequency >67%) followed by *Clytia linearis*, *D. quadridentata* and *S. tongensis* (frequency 34–67%), whereas three other alien species, *Eudendrium carneum*, *Eudendrium merulum* and *Sertularia marginata*, were less often observed (frequency 1–34%).

Oculina patagonica was the first alien scleractinian recorded in the Mediterranean Sea, possibly originating from the temperate Southwestern Atlantic (Zenetos *et al.* 2010). This coral is able to occupy both natural and artificial hard substrata, with a notable preference for the latter (Salomidi *et al.* 2013), and harbours are considered focal points for its dispersion (Rubio-Portillo *et al.* 2014).

Table 1. Alien species reported from Mediterranean marine caves. For each species data are given regarding the location, cave name, literature source, geographical area, cave zone, substrate type, origin, impact and pathway of introduction.

Taxa	Cave and location	Source	Area	Cave zone	Substrate	Origin	Impact	Pathway
Phylum Ochrophyta								
Ectocarpus siliculosus (Dillwyn) Lyngbye	Cabirol, Falco and Soffio caves (Sardinia)	MIATT-CoNISMa (2010)	BA	CE	H	Atl	Hi	Ac, Sh
Phylum Chlorophyta								
Caulerpa cylindracea Sonder	Scoglio di Fora cave (Lampedusa)	Alongi *et al.* (2012)	ST	CE	H	IP	Hi	Ac, Sh, Lm
Phylum Rhodophyta								
Acrothamnion preissii (Sonder)	Granchi cave (Sicily)	Alongi *et al.* (2012)	IS	CE	H	IP	Hi	Aq, Sh
Asparagopsis armata Harvey	Cabrera; Bisbe, Cabirol and Falco caves (Sardinia); Granchi, Gymnasium and Mazzere caves (Sicily); Scoglio di Fora and Taccio Vecchio caves (Lampedusa); small caves in Saronikos Gulf (Greece)	Uriz *et al.* (1993); MIATT-CoNISMa (2010); Alongi *et al.* (2012); present study	BA, ST, IS, SA	CE, SD	H	IP	Hi	Ac, Sh
Womersleyella setacea (Hollenberg)	Italian caves	Habitat Italia (2014)	Un	CE	H	IP	Hi	Sh
Phylum Cnidaria								
Class Anthozoa								
Oculina patagonica de Angelis 1908	Lebanese caves; small caves in Saronikos Gulf (Greece)	Bitar *et al.* (2007); Salomidi *et al.* (2013)	LB, SA	CE, SD	H	Atl	Hi	Sh
Class Hydrozoa								
Clytia linearis (Thorneley 1900)	Sa Catedral and Es Faralló caves (Mallorca); Bisbe, Falco and Galatea caves (Sardinia); Mitigliano cave (Gulf of Naples); Madonna, Scoglio di Fora and Taccio Vecchio caves (Lampedusa); Corvine, Granchi, Gymnasium, Lingua del Gigante and Mazzere caves (Sicily); Ciolo and Sifone caves (Apulia); Lebanese caves and tunnels	Gili & García-Rubies (1985); MIATT-CoNISMa (2010); Balduzzi *et al.* (1989); Moscatello & Belmonte (2007); Denitto *et al.* (2007, 2009); Morri *et al.* (2009)	BA, TS, ST, IS, LB	CE, SD, D*	H	Ct	L/U	Sh, Lm
Dynamena quadridentata (Ellis & Solander 1786)	Lebanese caves and tunnels	Morri *et al.* (2009)	LB	CE, SD	H	Ct	L/U	Lm
Eudendrium carneum Clarke 1882	Lebanese caves and tunnels	Morri *et al.* (2009)	LB	CE, SD	H	Ct	L/U	Sh, Lm

Table 1. Continued

Taxa	Cave and location	Source	Area	Cave zone	Substrate	Origin	Impact	Pathway
Eudendrium merulum Watson 1985	Falco cave (Sardinia); Madonna cave (Lampedusa); Lebanese caves and tunnels	MIATT-CoNISMa (2010); Morri *et al.* (2009)	BA, IS, LB	CE, SD	H	Ct	L/U	Sh
Filellum serratum (Clarke 1879)	Lebanese caves and tunnels	Morri *et al.* (2009)	LB	CE, SD	H	Ct	L/U	Sh
Mitrocomium medusiferum (Torrey 1902)	Falco cave (Sardinia); Corvine, Gymnasium and Lingua del Gigante caves (Sicily); Ciolo cave (Apulia)	MIATT-CoNISMa (2010); Denitto *et al.* (2009)	BA, IS	CE, SD	H	Ct	L/U	Sh
Sertularia marginata (Kirchenpauer 1864)	Lebanese caves and tunnels	Morri *et al.* (2009)	LB	CE, SD	H	Ct	L/U	Sh, Lm
Sertularia tongensis (Stechow 1919)	Lebanese caves and tunnels	Morri *et al.* (2009)	LB	CE, SD	H	IP	L/U	Sh, Lm
Phylum Mollusca								
Class Bivalvia								
Afrocardium richardi (Audouin 1826)	Selaata cave (Lebanon)	Crocetta *et al.* (2013a)	LB	Un (SD)	S	IP	L/U	Lm
Brachidontes pharaonis (P. Fischer 1870)[†]	Gulf of Catania cave (Sicily); Ramkine Island, Ras El Chakaa, Selaata and Tablieh caves (Lebanon)	Cantone *et al.* (1980); Crocetta *et al.* (2013a)	IS, LB	CE, SD	H, S	IP	Hi	Sh, Lm
Chama asperella Lamarck 1819	Jbail cave (Lebanon)	Crocetta *et al.* (2013a)	LB	Un (SD)	S	IP	L/U	Sh
Chama pacifica Broderip 1835	Ramkine Island, Ras El Chakaa, Chak El Hatab, Selaata, Kfar Abida and Jbail caves (Lebanon)	Crocetta *et al.* (2013a); Crocetta & Russo (2013)	LB	Un (SD)	H, S	IP	Hi	Sh
Malleus regula (Forsskål in Niebuhr 1775)	Ramkine Island, Ras El Chakaa, Chak El Hatab, Selaata, Kfar Abida and Jbail caves (Lebanon)	Crocetta *et al.* (2013a)	LB	Un (SD)	H, S	IP	L/U	Sh, Lm
Sphenia rueppellii A. Adams 1851	Kfar Abida cave (Lebanon)	Crocetta *et al.* (2013a)	LB	Un (SD)	H	IP	L/U	Sh
Spondylus spinosus Schreibers 1793	Selaata tunnel and cave (Lebanon)	Crocetta *et al.* (2013a)	LB	Un (SD)	H	IP	Hi	Sh
Teredo navalis Linnaeus 1758[†]	Ziva Voda cave (Croatia)	Novosel *et al.* (2007)	AN	D	S	Ct	Hi	Sh
Class Gastropoda								
Acteocina mucronata (Philippi 1849)	Selaata cave (Lebanon)	Crocetta *et al.* (2013b)	LB	Un (SD)	S	IP	L/U	Lm
Aplysia dactylomela Rang 1828	Small sciaphilous cave in Saadiyat (Lebanon)	Crocetta *et al.* (2013b)	LB	Un (SD)	H	Ct	Hi	Sh
Chelidonura fulvipunctata Baba, 1938	Cyclops Cave, Protaras (Cyprus)	Tsiakkiros & Zenetos (2011)	LB	Un (CE)	H	IP	L/U	Lm

Table 1. Continued

Taxa	Cave and location	Source	Area	Cave zone	Substrate	Origin	Impact	Pathway
Goniobranchus annulatus (Eliot 1904)	Ras El Chakaa and Raoucheh caves (Lebanon)	Crocetta *et al.* (2013b)	LB	CE	H	IP	L/U	Sh, Lm
Hypselodoris infucata (Rüppell & Leuckart, 1830)	Lebanese caves	Bitar *et al.* (2007)	LB	SD	Un	IP	L/U	Lm
Pleurobranchus forskalii Rüppell & Leuckart 1828	Chak El Hatab cave (Lebanon)	Crocetta *et al.* (2013b)	LB	Un (SD)	H	IP	L/U	Lm
Pyrunculus fourierii (Audouin 1826)	Jbail cave (Lebanon)	Crocetta *et al.* (2013b)	LB	Un (SD)	S	IP	L/U	Lm
Phylum Annelida								
Class Polychaeta								
Capitellethus dispar (Ehlers 1907)	Grotta Azzurra (Capo Palinuro)	Akoumianaki & Hughes (2004)	TS	SD	S	IP	L/U	Sh
Ficopomatus enigmaticus (Fauvel 1923)[†]	Orljak cave (Croatia); Bue Marino cave (Gulf of Orosei, East Sardinia)	Cukrov *et al.* (2010)	AN, TS	D	H	Ct	Hi	Ac, Sh
Hydroides heterocerus (Grube, 1868)	Rosh Haniqra shallow caves and tunnels	Ben-Eliahu & ten Hove (1992)	LB	CE	H	IP	L/U	Sh
Hydroides minax (Grube, 1878)	Rosh Haniqra shallow caves and tunnels	Ben-Eliahu & ten Hove (1992)	LB	CE	H	IP	L/U	Sh
Lysidice collaris Grube 1870	Gulf of Catania cave (Sicily)	Cantone *et al.* (1980)	IS	CE	H	IP	L/U	Sh
Notomastus aberans Day 1957	Grotta Azzurra (Capo Palinuro)	Akoumianaki & Hughes (2004)	TS	SD, D	S	IP	L/U	Lm
Eusyllis kupfferi Langerhans, 1879	Selaata and Ramkine Island caves (Lebanon)	Aguado & San Martín (2007)	LB	Un (SD)	H	Atl	L/U	Sh
Spirobranchus kraussii (Baird, 1865)	Lebanese caves	Bitar *et al.* (2007)	LB	SD	Un	IP	L/U	Sh
Syllis cf. *mayeri* Musco & Giangrande, 2005	Selaata and Ras el Chakaa caves (Lebanon)	Aguado & San Martín (2007)	LB	Un (SD)	H	Atl	L/U	Sh
Phylum Arthropoda								
Class Malacostraca								
order Amphipoda								
Monocorophium sextonae (Crawford 1937)	Bergeggi cave (Liguria)	Diviacco (1985)	LS	SD	H	Cr	Hi	Sh
order Decapoda								
Carupa tenuipes Dana, 1852	Dalyan (South Aegean Turkish coasts)	Yokes & Galil (2006)	SA	Un (SD)	H	IP	L/U	Lm
Herbstia nitida Manning & Holthuis 1981	Ciolo cave (Apulia)	Pastore & Denitto (2002); Denitto *et al.* (2010)	IS	SD	H	Atl	L/U	Sh
Percnon gibbesi (H. Milne Edwards 1853)	semi-submerged tunnels and small caves (Zakynthos Island)	present study	IS	CE, SD	H, S	Atl	Hi	Aq, Sh

Table 1. Continued

Taxa	Cave and location	Source	Area	Cave zone	Substrate	Origin	Impact	Pathway
Pilumnus minutus De Haan 1835	Fara cave (Lesvos Island)	present study	NA	CE	H	IP	L/U	Lm
Class Maxillopoda								
infra-class Cirripedia								
Balanus trigonus Darwin 1854	Bergeggi cave (Liguria)	Bianchi *et al.* (1986)	LS	TR	H	Ct	L/U	Sh
Phylum Bryozoa								
Bugula fulva Ryland 1960	Verde cave (Ustica Island); Granchi and Mazzere caves (Sicily)	Corriero *et al.* (1997); Rosso *et al.* (2013)	TS, IS	CE, SD, D	H	Cr	L/U	Sh
Microporella coronata (Audouin & Savigny 1826)	Ramkine Island and Chak El Hatab caves (Lebanon)	Harmelin *et al.* (2011)	LB	Un (SD)	H	IP	L/U	Lm
Microporella harmeri Hayward 1988	Selaata caves (Lebanon)	Harmelin *et al.* (2011)	LB	Un (SD)	H	Ct	L/U	Lm
Parasmittina egyptiaca (Waters 1909)	Ramkine Island, Chak El Hatab, Selaata, Kafar Abida and Tablieh shoal caves (Lebanon)	Harmelin *et al.* (2009)	LB	Un (SD)	H	IP	L/U	Lm
Parasmittina serruloides Harmelin, Bitar & Zibrowius 2009	Chak El Hatab and Selaata caves (Lebanon)	Harmelin *et al.* (2009)	LB	Un (SD)	H	IP	L/U	Lm
Schizoretepora hassi Harmelin, Bitar & Zibrowius 2007	Ras El Chakaa, Ramkine Island, Selaata, Chak El Hatab, Kafar Abida and Tablieh caves (Lebanon)	Harmelin *et al.* (2007)	LB	SD	H	IP	L/U	Lm
Smittina nitidissima (Hincks 1880)	Ramkine Island, Ras El Chakaa and Selaata caves (Lebanon)	Harmelin *et al.* (2009)	LB	Un (SD)	H	IP	L/U	Sh
Phylum Chordata								
Class Ascidiacea								
Herdmania momus (Savigny 1816)	Lebanese caves; Akhziv caves (Israel); Blue Cave (Kastelorizo Island)	Harmelin *et al.* (2007); Gewing *et al.* (2014); Katsanevakis *et al.* (2014a); present study	SA, LB	SD	H	IP	Hi	Sh
Phallusia nigra Savigny, 1816	Lebanese caves	Bitar *et al.* (2007)	LB	SD	H	Ct	L/U	Sh
Class Actinopterygii								

Table 1. Continued

Taxa	Cave and location	Source	Area	Cave zone	Substrate	Origin	Impact	Pathway
Pempheris rhomboidea Kossmann & Räuber, 1877	Levantine and South Aegean coasts of Turkey; El-Kouf National Park caves (Cyrenaica, Libya); small caves in Kastelorizo Island	Bilecenoğlu & Taşkavak (1999); Bilecenoglu (2010); Bazairi *et al.* (2013); present study	LB, LC, SA	CE, SD, D		IP	Hi	Lm
Sargocentron rubrum (Forsskål 1775)	Beirut (Lebanon); Levantine and South Aegean coasts of Turkey; several caves in Rhodes and Kastelorizo islands	Riedl (1966); Bilecenoglu (2010); Katsanevakis *et al.* (2014a); present study	LB, SA	CE, SD, D		IP	Hi	Lm
Siganus luridus (Rüppell 1829)	Taccio Vecchio cave (Lampedusa); small caves in Kastelorizo Island; shallow semi-submerged caves and tunnels in Zakynthos Island	MIATT-CoNISMa (2010); present study	ST, IS, SA	CE		IP	Hi	Lm

BA, Balearic Sea; LS, Ligurian Sea; TS, Tyrrhenian Sea; ST, Siculo-Tunisian Strait; IS, Ionian Sea; AN, North Adriatic; LC, Libyan Coast; NA, North Aegean; SA, South Aegean; LB, Levantine Basin; CE, cave entrance; SD, semi-dark zone; D, dark zone; TR, transitional zone between SD and D; H, hard substrate; S, soft substrate; Atl, Atlantic; IP, Red Sea/Indo-Pacific; Ct, circum(sub)tropical; Cr, cryptogenic; Hi, high; L/U, low/unknown; Ac, aquaculture; Aq, aquarium; Sh, shipping; Lm, Lessepsian migrant; Un, unspecified; †, recorded in anchialine caves; *, planktonic polyps.

Oculina patagonica was reported from shallow semi-dark caves (0–10 m) of Lebanon by Bitar *et al.* (2007). More recently, *O. patagonica* was found to occupy numerous small semi-dark caves, crevices and overhangs in Saronikos Bay (Salomidi *et al.* 2013 and authors' personal observations).

Molluscs

Fifteen alien molluscs (eight bivalves and seven gastropods) have so far been found in Mediterranean marine caves. The mussel *Brachidontes pharaonis* was recorded as *Brachidontes variabilis* (Krauss, 1848) by Cantone *et al.* (1980) in a semi-submerged cave in the Gulf of Catania (Ionian Sea). This is one of the earliest recorded and most successful Lessepsian migrants in the Mediterranean Sea, frequently found around Sicily (Zenetos *et al.* 2004).

The Indo-Pacific opisthobranch *Chelidonura fulvipunctata* was reported from Cyclops Cave (Protaras, Cyprus) by Tsiakkiros & Zenetos (2011), who photographed this nocturnal species near a rock crevice covered with macroalgae at a depth of 9 m.

Recently, seven alien opisthobranchs and seven alien bivalves, including *Brachidontes pharaonis*, were reported from the walls and soft sediment of several caves and tunnels in the Lebanese coasts (Bitar *et al.* 2007; Crocetta *et al.* 2013a,b; Crocetta & Russo 2013). It is notable that *B. pharaonis* was reported from a cave with freshwater spill. Additionally, skeletal remains of several valves and numerous tubes of the naval shipworm *Teredo navalis* were found on the muddy bottom of the anchialine cave Ziva Voda on Hvar Island (Adriatic Sea, Croatia) by Novosel *et al.* (2007). This cave, having no direct connections with the open sea and characterized by relatively stable cold-water temperatures year round (14.6–17.9 °C), harbours deep-sea species.

Polychaetes

Nine alien polychaetes are known from Mediterranean marine caves to date. *Lysidice collaris* was recorded by Cantone *et al.* (1980) at the entrance of a semi-submerged cave in the Gulf of Catania. *Hydroides heterocerus* and *Hydroides minax* were recorded in shallow (1–3 m) tunnels and caves off Rosh Haniqra in Israel by Ben-Eliahu & ten Hove (1992). Two more species, *Capitellethus dispar* and *Notomastus aberans*, were found in soft sediment on the sea bed of the semi-submerged cave Grotta Azzurra in Capo Palinuro (Akoumianaki & Hughes 2004). Both species were found in the semi-dark central hall of the cave, whereas *N. aberans* was also present in the dark transitional area situated between the semi-dark zone and the dark area, where sulphur springs are located.

The alien serpulid *Spirobranchus kraussii* and the syllids *Eusyllis kupfferi* and *Syllis* cf. *mayeri* were recently recorded in marine caves of Lebanon (Bitar *et al.* 2007; Aguado & San Martin 2007). The species *Branchiosyllis exilis* was also found by the latter study but is not considered a real alien because of its very wide distribution.

The Australian tubeworm *Ficopomatus enigmaticus* was found in two anchialine caves, characterized by low salinity values, one in the Northern Adriatic and the other on the Tyrrhenian coasts of Sardinia by Cukrov *et al.* (2010). This polychaete inhabited hard substrate surfaces in the entirely dark part of the caves, confirming its high adaptability potential. However, only scarce, solitary individuals were observed, by contrast to the typical gregarious growth form of the species.

Crustaceans

Six alien crustaceans have been found in Mediterranean marine caves. Two of them were reported from the marine cave of Bergeggi Marine Protected Area (MPA; Liguria, Italy); these are the cryptogenic species *Monocorophium sextonae*, recorded as *Corophium sextonae* Crawford, 1937, by Diviacco (1985), and the barnacle *Balanus trigonus*. The former was found in the semi-dark part of the cave and the second in the transitional zone between the semi-dark and dark assemblage.

Two alien decapods have been recorded in marine caves from the Aegean Sea. Yokes & Galil (2006) published a photograph of the nocturnal West Indo-Pacific crab *Carupa tenuipes* taken during a night dive in an 8-m depth cave on the South Aegean coast of Turkey. Additionally, a single juvenile specimen of the Indo-Pacific bristle crab *Pilumnus minutus* was found in a scraped sample from the coralligenous entrance zone of Fara cave (17 m) in Lesvos Island during the present study. The species had previously been reported from the coasts of Egypt (Galil *et al.* 2002 and references therein) as well as from the Aegean, Black Sea and Mediterranean coasts of Turkey (Ateş *et al.* 2010).

In the Ionian Sea, Denitto *et al.* (2010) found four specimens of the Guinean species *Herbstia nitida* at the semi-dark zone of Grotta di Ciolo cave in Apulia, under the sea-bed pebbles, together with juveniles of the native congeneric *Herbstia condyliata*. One more alien species, the copepod *Metacalanus acutioperculum*, was recorded from the exterior zone of the latter cave by Moscatello & Belmonte (2007). Additionally, during the present study, the invasive crab *Percnon gibbesi*, which is well established in the Ionian and Aegean seas (Katsanevakis *et al.* 2011), was observed to inhabit numerous shallow overhangs and semi-submerged tunnels of the National Marine Park of Zakynthos in Greece.

Bryozoans

Six alien bryozoans have been recorded so far from marine caves of the Mediterranean Sea. The cryptogenic *Bugula fulva* was reported from caves in MPAs of Sicily and Ustica, in the Ionian and Tyrrhenian Seas (Corriero *et al.* 1997; Rosso *et al.* 2013). Five alien bryozoans were found in semi-dark caves and tunnels of the Lebanese coasts by Harmelin *et al.* (2007, 2009, 2011); one of these, *Schizoretepora hassi*, was described as a new species from overhangs and caves in the area. This finding raised questions on the biogeographical origin of the new species, leading researchers to suggest that it constitutes (i) either a steno-endemic element restricted to this region or (ii) a Lessepsian migrant successfully established in sciaphilic rocky habitats of the area.

Tunicates

Two alien solitary ascidians have been recorded so far in marine caves of the Eastern Mediterranean basin. *Phallusia nigra* was found in shallow semi-dark caves of Lebanon (Bitar *et al.* 2007) whereas *Herdmania momus* has become a frequent dweller of marine caves in the same area (Harmelin *et al.* 2007) as well as in the Akhziv caves (3–5 m) in Israel (Gewing *et al.* 2014). The latter Lessepsian migrant was also recently found in the semi-submerged 'Blue cave' of Kastelorizo Island (Fig. 1A; Katsanevakis *et al.* 2014a). Although *Herd. momus* was initially restricted to artificial substrates (*e.g.* ports, piers, shipwrecks) and the lower sublittoral zone (20–30 m) of the Southeastern Levantine coasts, nowadays it seems to be well established in natural substrates of shallow waters, reaching an average of 2.85 individuals per m^2 in certain areas (Gewing *et al.* 2014).

Fishes

A picture of the Indo-Pacific red squirrelfish, *Sargocentron rubrum*, from a marine cave of Lebanon, published by Riedl (1966), makes this species the first alien recorded from Mediterranean caves. It is typically found in caves and crevices down to 60 m, along the Northern Levantine and the Southern Aegean coasts of Turkey (Bilecenoglu 2010). The red squirrelfish was frequently encountered, during the present study, in marine caves of Rhodes and Kastelorizo islands in the Southeastern Aegean.

Another Lessepsian migrant, the sweeper fish *Pempheris rhomboidea*, is quite common in caves across the Levantine and Southern Aegean coasts of Turkey (Bodrum peninsula), even sheltering in anchialine caves of Antalya Bay with a seasonal salinity of 0.6–5‰ (Bilecenoğlu & Taškavak 1999). The species was recently found to form small schools in cracks and marine caves of El-Kouf National Park (Cyrenaica, Libya) by Bazairi *et al.* (2013). In the Greek island of Kastelorizo, *P. rhomboidea* was observed in small mixed schools along with *Sa. rubrum* and the native cardinal fish *Apogon imberbis* (Fig. 1B–D). The sweeper fish is nocturnal, sheltering in large schools inside caves and crevices during daytime and leaving them at night in order to feed (Golani *et al.* 2002). According to the latter researchers the species experienced a population explosion almost immediately after invading the Mediterranean Sea.

The invasive rabbitfish *Siganus luridus* was recorded in the external zone of a cave in Lampedusa Island in the framework of a scientific project on the marine cave diversity of three Italian MPAs (MIATT-CoNISMa 2010). This species was also observed in the entrance zone of several overhangs and semi-submerged caves and tunnels in Kastelorizo and Zakynthos islands in the present study.

Finally, Guidetti *et al.* (2012) reported on the observation of the subtropical Eastern Atlantic fangtooth moray *Enchelycore anatina* near the entrance of a marine cave in Apulia (Ionian Sea). However, its presence in the area might be attributed to its gradual range expansion *via* the Gibraltar Strait (Guidetti *et al.* 2012; Zenetos *et al.* 2012).

Regional patterns and pathways of introduction

Most alien species (43) were recorded in marine caves from only one biogeographical area within the Mediterranean region, with only a few exhibiting a broad distributional range. This should not be attributed only to research effort, but also to the peculiarities of cave habitats. Marine caves are acknowledged for their high level of individuality and geographical fragmentation, which favour the survival of a broad range of taxa, thus presenting higher phylogenetic diversity than their surrounding rocky substrates (Gerovasileiou & Voultsiadou 2012).

The majority of alien species known from Mediterranean marine caves have been reported from the Southeastern Levantine coasts (37), followed by the Ionian Sea (11) (Fig. 2). These areas constitute the major gateways for the dispersal of Lessepsian migrants to the Western Mediterranean (Nunes *et al.* 2014). Shipping and Lessepsian migration were considered the most common pathways of introduction for cave alien biota (67.9% and 46.4%, respectively), followed by aquaculture (7.1%) and aquariums (3.6%). Most of the species (62.5%) originated

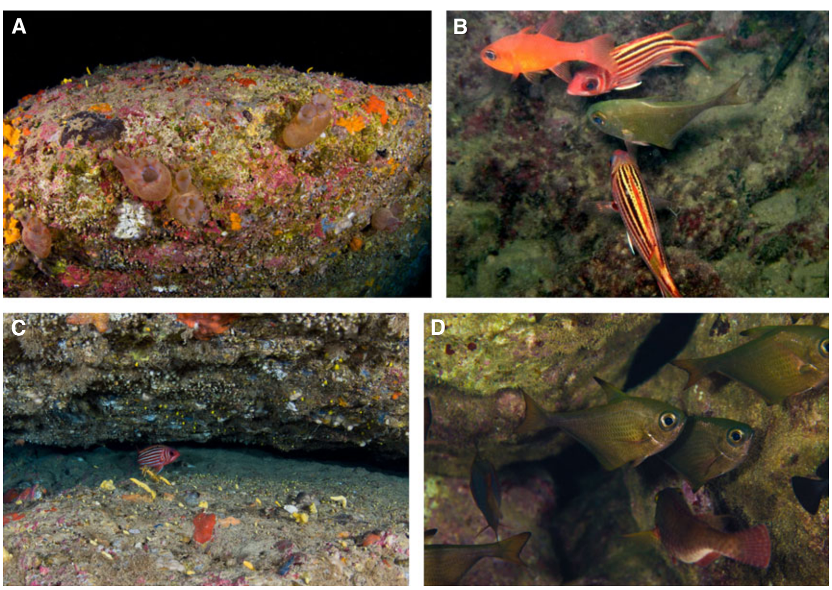

Fig. 1. (A): The tunicate *Herdmania momus*; (B): mixed school of *Apogon imberbis*, *Pempheris rhomboidea* and *Sargocentron rubrum*; (C): *S. rubrum* in an semi-dark cave community; and (D): *P. rhomboidea* in marine caves of Kastelorizo Island (photos a and c by Y. Issaris, b and d by G. Apostolopoulos).

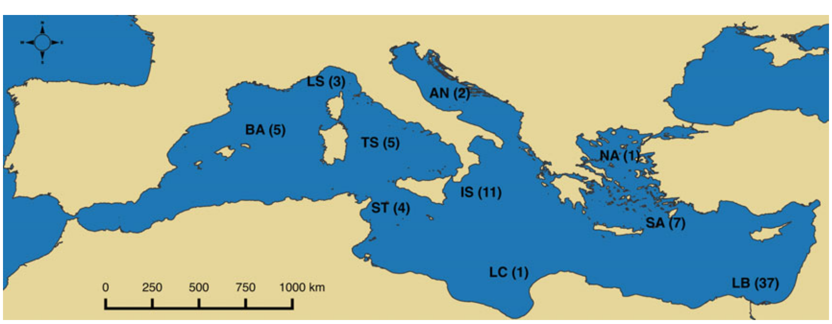

Fig. 2. Mediterranean areas in which alien species have been recorded from marine caves. Different Mediterranean areas are given with the following abbreviations: LB, Levantine Basin; SA, South Aegean; NA, North Aegean; IS, Ionian Sea; AN, North Adriatic; LC, Libyan coast; ST, Siculo-Tunisian Strait; TS, Tyrrhenian Sea; LS, Ligurian Sea; BA, Balearic Sea. Numbers of aliens in each area are given in parentheses.

from the Red Sea/Indo-Pacific Ocean. Species with circum(sub)tropical distribution accounted for 23.2% of the alien cave biota. Species originating from the Atlantic Ocean accounted for 10.7%, and two species were cryptogenic.

However, these percentages, as well as the taxonomical composition of biota, differed amongst Mediterranean regions (Fig. 3). Alien biota from EMED caves belonged to eight major groups, with mollusc (14), cnidarian (eight) and bryozoan (six) species dominating. In the other three Mediterranean regions species were more evenly distributed amongst taxa. It is interesting that alien fish species have not yet occupied any caves in the WMED. Marine caves in ADRIA had the lowest number of alien species (two), possibly because of the locally higher proportion of anchialine caves, submarine springs and vertical pits, which encompass stratified cold-water masses (Surić *et al.* 2010).

The current update of overall Mediterranean alien diversity added 32 species (Appendix S1); thus the total alien biota of the Mediterranean Sea numbers ~1020 species (WMED: 315; CMED: 265; ADRIA: 198; EMED: 799). New additions were mainly molluscs (11), crustaceans (eight), polychaetes (four) and fishes (four). A comparison between the total alien biodiversity of the four Mediterranean regions and that of caves revealed similar patterns with regard to species richness (Fig. 4) and biogeographical origin (see Zenetos *et al.* 2010), with the exception of ADRIA, where only two circumtropical species have been found. In the EMED, Indo-Pacific species dominated in both cases, followed by those with circumtropical distribution, whereas Atlantic species con-

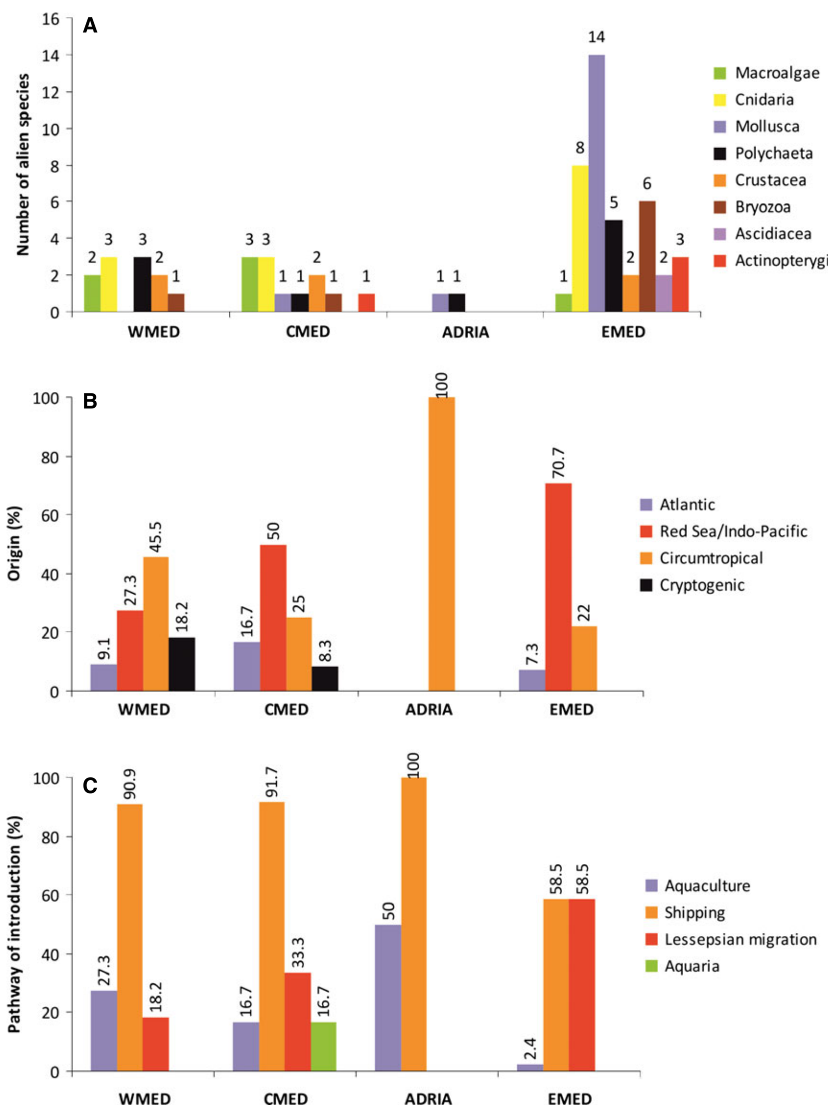

Fig. 3. Regional patterns for (A): the taxonomic composition, (B): origin and (C): pathway of introduction of alien species in Mediterranean marine caves. In the latter graph, percentages add to more than 100% because some species are linked to more than one pathway. WMED, Western Mediterranean; CMED, Central Mediterranean; ADRIA, Adriatic; EMED, Eastern Mediterranean.

stituted a minimal percentage. In the CMED, a similar pattern was observed with a slightly higher contribution of Atlantic species in cave habitats. The greatest difference between the origin of the total and cave alien biota was observed in the WMED where circumtropical species were over-represented in the marine cave environment. Species with Indo-Pacific origin and Atlantic species made approximately similar contributions in both cases.

Shipping was found to be the most likely pathway of introduction for the marine cave alien biota of all regions, except for the EMED, where Lessepsian migration is equally probable. The contribution of the latter pathway decreased westwards whereas the opposite was found for aquaculture. These findings are in accordance with general trends described for the total alien biodiversity of the Mediterranean Sea (Zenetos *et al.* 2012). The role of shipping as a possible pathway of introduction for alien species in the marine cave habitat is also supported by the fact that many semi-submerged caves are often visited by tourist boats; an example is Grotta Azzurra, which is frequently visited by tourist boats departing from the neighbouring harbour of Palinuro; in both locations alien species were recorded (*e.g.* Gambi *et al.* 2008).

Alien species and ecological gradients in marine caves

The majority of alien species reported from Mediterranean caves were observed at the entrance (25) and semi-dark (42) zones of shallow and/or semi-submerged caves and tunnels. These cave types and sectors are situated in a high hydrodynamic regime, with high levels of water circulation as they are topographically exposed to storm and wave action (Riedl 1966).

By contrast, only eight alien species have been recorded from the dark interior of Mediterranean caves. Totally dark caves are considered to be extreme and highly selective environments, characterized by increased levels of oligotrophy and confinement (Harmelin *et al.* 1985; Bianchi & Morri 1994). The dispersal of the biota in the dark cave interior primarily depends on water circulation but multiple environmental variables determine their post-settlement survival, thus excluding several species (Benedetti-Cecchi *et al.* 1996; Harmelin 1997; Denitto *et al.* 2007). Therefore, this unfavourable habitat type seems to be naturally protected from impacts related to opportunistic invasive species, at least to a certain point. This has been also suggested for terrestrial caves, where low-ecosystem productivity may function as a mitigating factor in controlling exotic cavernicoles (Reeves 1999).

Apart from the light and confinement gradients that typically characterize marine cave environments, the existence of cave-specific features such as freshwater springs and thermal vents can increase habitat complexity. Consequently, anchialine caves with stratified water masses often harbour unique biodiversity, consisting of several stygobiotic (cave-exclusive) species (Iliffe & Kornicker 2009), whereas the presence of warm-water sulphur springs in some caves (*e.g.* Grotta Azzurra, Tyrrhenian Sea) supports an exceptional chemosynthetic ecosystem of great scientific interest (Southward *et al.* 1996). It is noteworthy that four alien species were found in anchialine caves (*Ficopomatus enigmaticus*, *Brachidontes pharaonis* and *P. rhomboidea* in shallow and/or semi-submerged caves and *Teredo navalis* in a cave having no direct connection with the open sea), whereas two were recorded in the sediment of the semi-dark and dark sectors of Grotta Azzurra. This illustrates the high adaptability potential of some alien species under variable environmental conditions (Cukrov *et al.* 2010). In the relevant literature there are no data that indicate any impacts of alien species on the local diversity of these caves.

Alien species and marine cave biodiversity

Recent overviews of the existing knowledge on Mediterranean marine cave biodiversity have shown that marine caves harbour ~13% of the Mediterranean biota, with a considerable representation of several sciaphilic taxa (Ger-

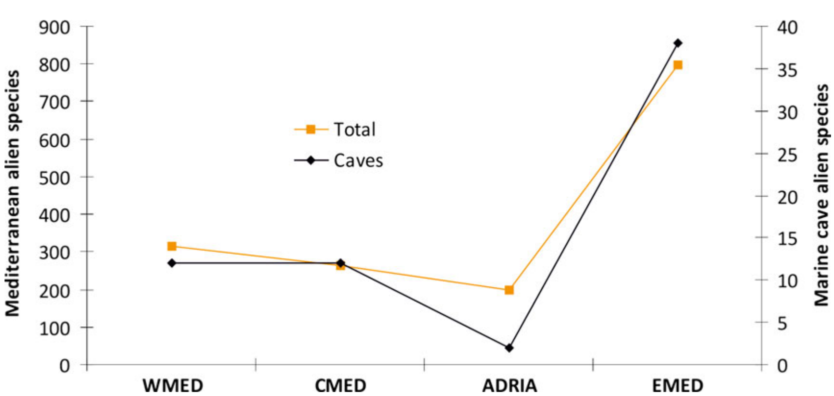

Fig. 4. Regional patterns for the total and marine cave alien species richness of the Mediterranean Sea. WMED, Western Mediterranean; CMED, Central Mediterranean; ADRIA, Adriatic; EMED, Eastern Mediterranean.

ovasileiou & Voultsiadou 2012, 2014). However, the vast majority of the species recorded in the Mediterranean caves are stygophilic or stygoxenes, with cave-exclusive biota constituting only 3% of the known biodiversity (V. Gerovasileiou & E. Voultsiadou, unpublished data). This general trend is also reflected in the marine cave alien biota, which have been recorded in various soft and/or hard substrate types of habitats, including artificial surfaces (*e.g.* Bitar *et al.* 2007; Harmelin *et al.* 2009; Morri *et al.* 2009; Gewing *et al.* 2014). The majority of alien species recorded in marine caves (78.6%) were found on hard substrates (Table 1).

However, the alien diversity in Mediterranean marine caves is possibly higher than what we actually know. This hypothesis is supported by the difficulties involved in the identification of many specimens and some authors have suggested that their unidentified material might be alien species (*e.g.* Rosso *et al.* 2013). Other pieces of evidence are the recent finding of small-sized cryptic alien species, suggesting that several others might have been overlooked in the past owing to their small size (Denitto *et al.* 2010) and the finding of a dozen alien species in cave sediments despite the very low number of studies focusing on soft-substrate cave diversity (*e.g.* Bianchi & Morri 2003; Akoumianaki & Hughes 2004; Todaro *et al.* 2006; Navarro-Barranco *et al.* 2012).

Moreover, the fauna of the Southeastern Mediterranean, an area extremely susceptible to marine biological invasions through Lessepsian migration (Nunes *et al.* 2014), remains largely unknown, especially in regard to the sciaphilic sessile biota. Many sessile species, having entered the Mediterranean Sea through shipping, were established initially on artificial substrates and then progressively developed populations on natural substrates in shallow and deep waters (Gewing *et al.* 2014). Recent studies in semi-dark caves and tunnels of Lebanon have remarkably increased our knowledge on the region's biodiversity, revealing several new, endemic and alien species (Bitar *et al.* 2007; Harmelin *et al.* 2007; Morri *et al.* 2009; Crocetta *et al.* 2013a,b). Study of the local bryozoan fauna showed a remarkable representation of species belonging to genera typical of the tropical and subtropical regions; this biogeographical discrepancy was partly attributed to the input of alien species (Harmelin *et al.* 2009, 2011). Such findings are in accordance with other zoogeographic studies on hard substrate sessile biota that have revealed that the proportion of warm-water species increases from the Northwestern to the Southeastern Mediterranean, reaching their highest proportions in the South Aegean and the Levantine seas (Boero & Bouillon 1993; Gerovasileiou & Voultsiadou 2012). Taxonomic difficulties in the identification of several taxa (*e.g.* foraminiferans, sponges, hydrozoans and bryozoans) may be an impediment to the discovery of unknown endemic or alien species, causing under-estimation of both indigenous and alien diversity. It is interesting that no alien Porifera have been recorded so far from Levantine caves (but see Pérez *et al.* 2004) despite sponges constituting one of the dominant animal groups in this habitat (Gerovasileiou & Voultsiadou 2012, 2014). Thus, it is reasonable to assume that the actual number of alien species in marine caves of the Mediterranean Sea is much higher than we know.

Several alien sessile species seem to be well established in marine caves and overhangs of the Levantine basin (Harmelin *et al.* 2007). According to our data, alien species were reported in caves from 11 sites of the Southeastern Levantine, which corresponds to more than 80% of the marine caves known to exist in the area (Giakoumi *et al.* 2013). A comparative study between recent and historical data on the molluscan fauna of this region, including caves and tunnels, revealed that many common habitat-forming bivalves previously known to exist in the area were scarce or totally absent, possibly replaced by the aliens *Brachidontes pharaonis*, *Spondylus spinosus* and *Chama pacifica* (Crocetta *et al.* 2013a). Local extinction of native Mediterranean species owing to the presence of invasive species (*i.e.* the chlorophyte *Caulerpa cylindracea*, the Kuruma prawn *Marsupenaeus japonicus*, and the fishes *Fistularia commersonii*, *Siganus luridus* and *Siganus rivulatus*) has taken place in parts of the Aegean, Ionian and Levantine seas (Voultsiadou *et al.* 2013 and references therein). Furthermore, water temperature anomalies related to climate change, which have been found to negatively affect marine cave communities in the Western Mediterranean basin (Chevaldonné & Lejeusne 2003; Parravicini *et al.* 2010), might constitute an additional vector for the introduction of alien species into these poorly resilient ecosystems.

Concerning the marine cave ichthyofauna, so far there is no evidence of competition between native (*e.g. Apogon imberbis*) and alien species (Otero *et al.* 2013; authors' observations). In addition to the recorded fishes, another four non-indigenous species that have entered the Mediterranean Sea are known to shelter in caves, coral reef cavities and holes within their natural range of distribution; these are the cardinalfish *Apogonichthyoides pharaonis*, the spot-fin porcupinefish *Diodon hystrix*, the arrow bulleye *Priacanthus sagittarius* and the stonefish *Synanceia verrucosa* (Golani *et al.* 2002; Froese & Pauly 2014). For the time being, there are no data on the presence of these species in Mediterranean caves but given their ecological habits, they constitute potential newcomers in the local cave habitats. Recent cave records of the species *Sargocentron rubrum* and *P. rhomboidea* from the Southeastern

Aegean, Levantine Sea and Cyrenaica in Libya, where numerous caves exist, may indicate that the westward expansion of these typical cave-dwelling animals is related to the availability of suitable habitats. The latter two fishes as well as *A. pharaonis* and *D. hystrix* have nocturnal habits, hiding in small caves during the day and moving out at night in order to feed (Froese & Pauly 2014). These daily horizontal migrations, specifically by species that form large schools (*e.g. P. rhomboidea*), could affect the cavernicolous sessile biota by increased incoming organic matter in the naturally oligotrophic cave habitats (Bianchi *et al.* 2003; Otero *et al.* 2013). Similar migration patterns by native swarm-forming mysids have been shown to influence energy transfer from the open sea to the confined cave environment (Coma *et al.* 1997).

Our review showed that 32.1% of the alien species recorded from marine caves are among those considered to have a high impact on the native biodiversity of the Mediterranean (EASIN 2014); Nineteen of the species were included on a list of the worst invasives of the Mediterranean (Streftaris & Zenetos 2006) and 13 were documented to be among the marine aliens with the most impact at a pan-European level (Katsanevakis *et al.* 2014b). The rest of the species have low or unknown impacts. For the time being, the existing data show that alien species have not severely impacted marine cave communities, as far as the Northern and Western Mediterranean areas are concerned. However, the high number of alien species in marine caves of the Southeastern Mediterranean constitutes a potential threat.

Given the absence of data depicting the previous ecological state of the cave habitat in this area, which could provide a basis for its monitoring, it is difficult to evaluate the level of impact on the native cave biota. Quantitative surveys in the ‘invaded’ caves and comparisons with pre-existing data (see Bianchi *et al.* 2014), if any (*e.g.* grey literature and photographic/video material), or with ‘pristine’ caves in adjacent areas (*e.g.* Cyprus, Levantine coasts of Turkey, South Aegean and Libyan coasts) are needed in order to evaluate possible impacts and to set regional priorities for their conservation.

Conclusions

Alien species have been successfully established in various habitat types, including Mediterranean marine caves. According to the existing data, the more illuminated sections of caves (*i.e.* entrance and semi-dark zones) and the types of caves with high hydrodynamic regimes (*i.e.* shallow and/or semi-submerged caves and tunnels) are more susceptible to marine biological invasions than darker sections of caves and caves with lesser hydrodynamic regimes. In spite of the locally unfavourable environmental conditions, a few alien species with high adaptability potential are able to colonize the more confined dark cave sectors or even caves of the anchialine type. At present none of the alien species recorded in marine caves are exclusive to this habitat, and there are no data indicating any impact of these species on native cavernicolous diversity; nevertheless, the frequent presence of aliens in the Southeastern Mediterranean basin, where there is no knowledge of the pre-existing conditions, should be further surveyed and monitored. The resemblance of patterns and trends between the marine cave alien and the overall Mediterranean alien biota corroborates previous findings on the high local representativeness of Mediterranean cave biodiversity. Similar studies are needed on other habitat types which might be used by marine aliens as stepping stones for their further expansion in the Mediterranean Sea, as well as on vulnerable priority habitats with high conservation value.

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