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Introduced species in Mediterranean marine caves: an increasing but neglected threat

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Abstract

Marine caves are protected habitats with high biodiversity and low ecological resilience, vulnerable to multiple pressures including biological invasions. Therefore, comprehensive lists of alien species in sea caves and assessments of their impacts are urgently needed. This study aimed to provide an updated and validated list of introduced species in marine caves of the Mediterranean Sea based on the latest available checklist (2014). The number of introduced species in the updated list (December 2022 status) has doubled in the last eight years. The updated checklist includes 126 species (107 alien, 15 cryptogenic, two crypto-expanding, and two questionable) belonging to 12 phyla. The highest number of introduced species in caves was evidenced in the eastern Mediterranean (105), specifically in the Levantine (99) and the Aegean (34) ecoregions. Most introduced species originated from the Indo-Pacific. Most species entered the Mediterranean Sea through the Suez Canal, followed by species transferred *via* vessels. Most introduced species were found at the entrance and in the semi-dark zone of caves (60 and 52 species, respectively), with only 19 species being reported from the dark zone. Approximately 28% of the introduced species have a high impact on ecosystems, including nine of the ten worst invasive species in the Mediterranean Sea. Despite the lack of data on the impact of introduced species on marine cave biodiversity, given their high species richness and the recently reported population explosions of some alien fish in the eastern Mediterranean, our results highlight the need for continuous inventorying and monitoring.

Keywords: Alien species; non-indigenous species; sea caves; Mediterranean Sea.

Introduction

Biological invasions are one of the causes of biodiversity loss (Pyšek *et al*., 2013; Brondizio *et al*., 2019). During the last century, biological invasions have contributed to the extinction of 62% of amphibians, reptiles, birds, and mammals that went extinct (Bellard *et al*., 2016). Climate change, habitat disturbance, increased global trade, and socio-economic change are expected to play a major role in biological invasions and in the future shift of species distributions (Bellard *et al*., 2018; Roura-Pascual *et al*., 2021). The frequency and magnitude of introductions of alien (i.e., non-indigenous) species and the impacts caused by biological invasions will likely increase in the future (Seebens *et al*., 2021; Essl *et al*., 2020). The most efficient way to combat biological invasions is the prevention of further introductions by managing their major pathways because, once an alien species has been established in a new environment, its eradication is very costly and often impossible (Puth & Post, 2005). Developing strategies to prevent further introductions requires knowledge of the biology and ecology of the newly introduced species, evaluation of introduction pathways, and risk assessments. Comprehensive and updated lists of alien species and their invasiveness in a given area or habitat are pivotal in this direction.

During the last decades, significant efforts and collaborative initiatives have led to the development of comprehensive databases and updated checklists of marine alien species at global, regional, or national levels (e.g., Katsanevakis *et al*., 2015; AquaNIS, 2015; Zenetos *et al*., 2015a; 2022a; Costello *et al*., 2021), and specifically in the Mediterranean Sea, which is considered a global hotspot for biological invasions (Katsanevakis *et al*., 2014a;

Korpinen *et al*., 2019; Costello *et al*., 2021). However, ecological information about alien species (e.g., habitat or substrate type, depth) is often scarce or even lacking from most published and online databases. Such information is useful for the effective monitoring, management, and protection of habitats of high scientific and conservation importance, as well as for the early detection of new alien species records with specific ecological requirements (Gerovasileiou *et al*., 2016).

Marine caves constitute one of the most striking features of Mediterranean rocky coastlines, where geological processes such as karstic phenomena have led to the formation of many marine and anchialine cave systems, either semi-submerged or entirely submerged (Gerovasileiou & Bianchi, 2021). More than 3000 marine caves are known from the Mediterranean Sea, densely concentrated on rocky islands and peninsulas along its northern coasts (Giakoumi *et al*., 2013; Sini *et al*., 2017; Gerovasileiou & Bianchi, 2021). However, the actual number of sea caves is assumed to be much higher, as many have never been surveyed or described (see, for a striking example, Montefalcone *et al*., 2022). These habitats are protected by the European Union's Habitats Directive (92/43/EEC) and the Barcelona Convention under the Dark Habitats Action Plan (UNEP-MAP-RAC/SPA, 2015) and have been widely acknowledged for their biological wealth, harbouring rare, endemic, and protected species (Ouerghi *et al*., 2019; Gerovasileiou & Bianchi, 2021). For this reason, Mediterranean marine caves have been characterised as "refuge habitats" (Harmelin *et al*., 1985) and "biodiversity reservoirs" within a biodiversity hotspot (Gerovasileiou & Voultsiadou, 2012, 2014).

According to the latest biodiversity census for this habitat, approximately 2370 taxa have been reported from approximately 400 marine caves in 15 Mediterranean countries (Gerovasileiou & Bianchi, 2021). Given the large number of alien species in the Mediterranean Sea – approximately 1000 according to Zenetos *et al*. (2022b) – and the broad distribution of marine caves in the eastern Mediterranean basin (Gerovasileiou *et al*., 2015; Sini *et al*., 2017; Öztürk, 2019), alien species could not be missing from this particular habitat. The occurrence of introduced species in Mediterranean marine caves was reviewed in 2014 by Gerovasileiou *et al*. (2016), who listed 56 alien and cryptogenic species from approximately 50 caves and tunnels, mainly in the Levantine Sea. Approximately one-third of these species were among those with the highest negative impact on a pan-European level at that time (Katsanevakis *et al*., 2014a and EASIN data), including nine species listed among the worst invasives in the Mediterranean Sea (Streftaris & Zenetos, 2006). However, until today it remains unknown and undocumented if marine alien species negatively affect native cave biota, despite the increasing number of records and the population explosion of some alien species in sea caves of the eastern Mediterranean Sea (Gerovasileiou *et al*., 2016; Digenis *et al*., 2021a, 2022a).

Subterranean ecosystems, including marine and anchialine caves, are generally the most understudied ecosystems on Earth, mainly due to multiple impediments to scientific research and monitoring, such as no or limited accessibility, and are often overlooked in conservation agendas (Ficetola *et al*., 2019; Keith *et al*., 2022; Mammola *et al*., 2022). Marine cave ecosystems have low ecological resilience (Harmelin *et al*., 1985; Rastorgueff *et al*., 2015) and are threatened by multiple global and local pressures, such as seawater warming and disturbances caused by coastal interventions, unregulated tourism, and pollution (Giakoumi *et al*., 2013; Montefalcone *et al*., 2018; Gerovasileiou & Bianchi, 2021). This fact – coupled with their unique biodiversity – suggests that marine caves can be particularly vulnerable to biological invasions. Extensive efforts are urgently needed to investigate the potential impact on native biota.

This study aimed to provide an updated and validated list of introduced species from Mediterranean marine caves, eight years after the previous assessment, along with current patterns of spatial distribution and introductions, with the ultimate goal of raising awareness of this increasing yet neglected threat.

Materials and Methods

Starting from the latest available checklist of alien and cryptogenic species reported from Mediterranean marine caves, published by Gerovasileiou *et al*. (2016) (2014 status), we prepared an updated checklist by: (1) performing a screening of peer-reviewed and grey literature (e.g., books, conference papers, project reports, and online databases/websites) on Mediterranean marine caves published by December 2022; (2) assessing the data on alien species records from marine caves (when information on habitat was available), archived in the off-line database of the Hellenic Centre for Marine Research (HCMR)/European Environment Agency (EEA), which resulted from the latest inventories by Zenetos *et al*. (2012, 2022b); and (3) obtaining new data from fieldwork surveys carried out in marine caves of the Ionian, Aegean and Levantine seas (Katsanevakis *et al*., 2020a).

All the species in the compiled list (Annex I - Supplementary material) were checked for (i) nomenclature against the World Register of Marine Species (WoRMS Editorial Board, 2022); (ii) alien status according to Zenetos *et al*. (2017, 2022b), Zenetos & Galanidi (2020), and the European Alien Species Information Network (EASIN, 2022), (iii) native distribution range (possible origin), according to Tsiamis *et al*. (2018), WoRMS, and SeaLifeBase (Palomares & Pauly, 2022), and (iv) level of impact (high/low) according to EASIN (2022) and recent literature (Tsirintanis *et al*., 2022).

The term 'introduced' is here used in the broad sense (*sensu lato*) in order to include alien species (*sensu* Essl *et al*., 2018) but also cryptogenic (i.e., species that cannot be easily demonstrated as being either introduced or native) and crypto-expanding (i.e., those for which it remains to be clarified if they have naturally expanded their range or their introduction is linked to human activities), as well as a few species whose status remains questionable (Zenetos *et al*., 2017, 2018, 2020, 2022b). For alien

species, we gathered information on the most plausible pathways of primary introduction in the Mediterranean Sea according to the classification of the Convention on Biological Diversity (CBD, 2014), as modified by Pergl *et al*. (2020). These are:

COR = Corridor: interconnected waterways/basins/seas; Suez Canal;

EC = Escape from confinement;

REL = Release in nature: aquaculture/mariculture; intentional release of live organisms from confinement, including the disposal of aquaria-kept species into the wild;

TC = Transport-Contaminant: contaminated nursery material; contaminated bait; food contaminant (including live food); contaminant on animals (except parasites, species transported by host/vector); parasites on animals (including species transported by host and vector); contaminant on plants (except parasites, species transported by host/vector); parasites on plants (including species transported by host and vector);

TS = Transport-Stowaway: ship/boat hull fouling; other means of transport; angling/fishing equipment; hitchhikers on ship/boat (excluding ballast water and hull fouling); ship/boat ballast water;

When available, we also recorded information on the distribution of introduced species in marine caves [i.e., species that were recorded at the entrance of the cave (CE), in the semi-dark zone (SD), or the dark zone (D)]. Macroalgae for which there was no information regarding ecological cave zones were all assigned to the cave entrance, where they would most likely occur (although, in a few cases, macroalgae were also reported from the semi-dark zone of caves). To explore patterns of spatial distribution and pathways of introductions at the regional scale, the presence of introduced species in Mediterranean marine caves was assigned to four marine regions according to the Marine Strategy Framework Directive (MSFD) classification (EU, 2008), namely: Western Mediterranean (WMED), Central Mediterranean (CMED), Adriatic (ADRIA) and Eastern Mediterranean (EMED). These regions were further subdivided into seven ecoregions *sensu* Spalding *et al*. (2007), namely: Alboran Sea (AL), Western Mediterranean (WM), Tunisian Plateau/Gulf of Sidra (TP), Ionian Sea (IS), Adriatic Sea (AD), Aegean Sea (AS), and Levantine Sea (LS). For the native distribution range assessment, all introduced species were assigned to global marine biogeographic realms, according to Spalding *et al*. (2007). All graphs were prepared in R version 4.1.3 (R Core Team, 2022).

Results and Discussion

Research effort overview

The literature review resulted in 81 sources (Annex II - Supplementary material) containing information on the occurrence of introduced species in Mediterranean marine caves. However, only a few studies (e.g., Denitto *et al*., 2010; Harmelin, 2014; Gerovasileiou *et al*., 2016; Rosso *et al*., 2018; Galil & Goren, 2019; Digenis *et al*., 2021a, b, 2022a, b; Florido *et al*., 2022) were focused explicitly on introduced species in marine cave habitats. Most records were reported in the context of ecological and biodiversity assessments conducted in particular in the eastern Mediterranean Sea (e.g., Castelló *et al*., 2020; Crocetta *et al*., 2020), or/and in the frame of collective articles of *Mediterranean Marine Science* (Katsanevakis *et al*., 2014b; Crocetta *et al*., 2015, 2020; Dailianis *et al*., 2016; Mytilineou *et al*., 2016; Bariche *et al*., 2020; Ragkousis *et al*., 2020) and collaborative data papers (Katsanevakis *et al*., 2020b; Ragkousis *et al*., submitted). To this end, the latter two types of publications provide an important platform to report new records from specific areas and habitats that could easily be overlooked when reported as part of general studies. Two other important sources of data worth mentioning are a recently published book on marine caves of the eastern Mediterranean Sea (Öztürk, 2019), which reported many records from Turkey and the Levantine Sea, and two reports on the ecological characterisation of sites of conservation interest from Lebanon (RAC/SPA–UNEP/MAP, 2014; SPA/RAC–UN Environment/MAP, 2017).

Current status of introduced species

The updated checklist (December 2022 status) of introduced species in Mediterranean marine caves includes 126 species, among which 107 are alien, 15 cryptogenic, two crypto-expanding, and two questionable (Annex I - Supplementary material). The number of species on the updated list has more than doubled (2.2 times higher) since the previous (2014) census of alien and cryptogenic species in Mediterranean marine caves (Gerovasileiou *et al*. 2016). This result suggests an increase of 225% in the number of introduced species in the last eight years. Nevertheless, we cannot exclude the possibility that the increase is partly the result of increased research effort and number of targeted surveys on introduced species in marine caves.

The species on the updated list belong to 12 phyla, i.e., in decreasing order from the most species-rich phylum, 26 Mollusca (15 Gastropoda, ten Bivalvia, and one Cephalopoda), 25 Chordata (18 Actinopterygii and seven Ascidiacea), 16 Arthropoda (all Crustacea), 16 Bryozoa, ten Cnidaria (eight Hydrozoa, one Scyphozoa, and one Anthozoa), ten Annelida (nine Polychaeta and one Sipuncula), eight Rhodophyta, six Chlorophyta, four Ochrophyta, three Echinodermata (one Asteroidea, one Echinoidea, and one Holothuroidea), one Foraminifera, and one Porifera (Annex I - Supplementary material).

Regional patterns and spatial distributions

In line with the previous results, the majority of introduced species were reported from marine caves of the eastern Mediterranean (105 species: 83.3%), in particular

from the Levantine (99 species) and Aegean ecoregions (34 species) (Fig. 1). A much lower number of species was documented in the western (19) and central (18) Mediterranean, whereas in the Adriatic Sea caves only five species were reported. The highest number of introduced phyla was found in the eastern Mediterranean (12). Introduced species in the western and central Mediterranean belong to eight phyla; only four phyla were found in the Adriatic (Fig. 2). Mollusca (13 Gastropoda, nine Bivalvia, and one Cephalopoda) and Chordata (18 Actinopterygii and five Ascidiacea) prevailed in the eastern Mediterranean in terms of species number (23 species each). In the central Mediterranean, most of the introduced species belonged to Chordata (four Actinopterygii and one Ascidiacea) and in the western Mediterranean to Arthropoda (Fig. 2). No introduced fishes have been observed in caves of the western Mediterranean and the Adriatic Sea. This could be attributed either to the limited research effort regarding motile species in marine caves or to the fact that most alien fish species have not yet reached or have been rarely reported from the aforementioned regions (Katsanevakis *et al*., 2014a). For instance, the lionfish *Pterois miles* (Bennett, 1828) was only recently reported from rocky beds of the Adriatic Sea (Dragičević *et al*., 2021), and thus it is expected to be observed in marine caves in the near future.

The number of alien species in marine caves in the different Mediterranean regions follows a similar pattern as that of the total number of marine alien species (December 2022 status) (Fig. 3). This result agrees with the findings of the previous census (Gerovasileiou *et al*., 2016), corroborating that marine caves harbour a representative fraction of the Mediterranean xenodiversity. Alien species in marine caves represent 11.9% of the total number of alien species in the eastern Mediterranean – more than double (2.6 times higher) the percentage of alien species reported in the previous census – and less than 5% of the alien biodiversity in the other three Mediterranean regions.

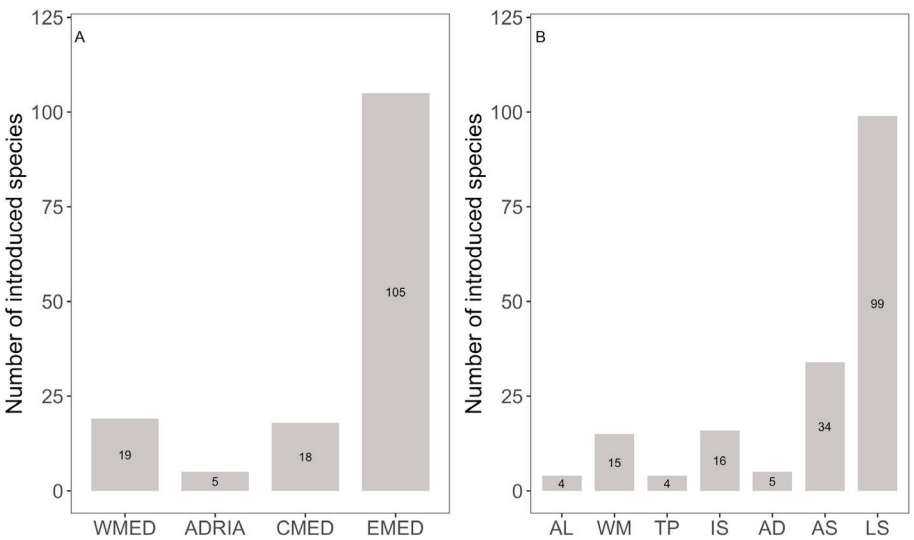

Fig. 1: Number of introduced species in marine caves of different (A) MSFD regions: WMED = Western Mediterranean; ADRIA = Adriatic; CMED = Central Mediterranean; EMED = Eastern Mediterranean; and (B) ecoregions: AL = Alboran Sea; WM = Western Mediterranean; TP = Tunisian Plateau/Gulf of Sidra; IS = Ionian Sea; AD = Adriatic Sea; AS = Aegean Sea; LS = Levantine Sea.

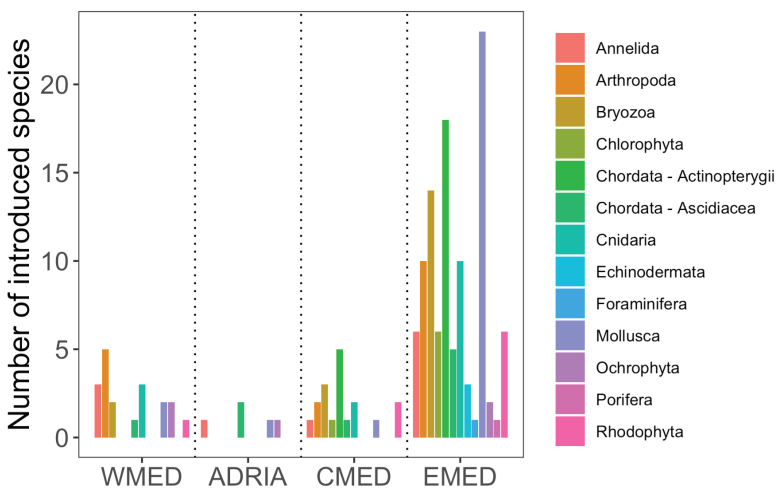

Fig. 2: Number of introduced species by phylum (and class for Chordata) in marine caves of different Mediterranean MSFD regions: WMED = Western Mediterranean; ADRIA = Adriatic; CMED = Central Mediterranean; EMED = Eastern Mediterranean.

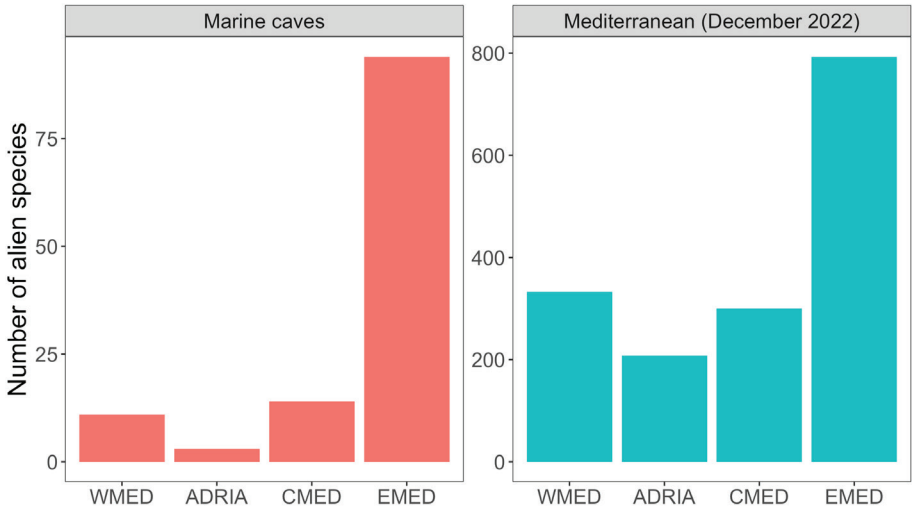

Fig. 3: Regional patterns for the total number of alien species (December 2022 status) and those recorded in marine caves by Mediterranean region: WMED = Western Mediterranean; ADRIA = Adriatic; CMED = Central Mediterranean; EMED = Eastern Mediterranean.

Introduced species were recorded in sea caves of 11 Mediterranean countries (of the 15 countries where this habitat is known to occur according to Gerovasileiou & Bianchi, 2021), namely in the following countries (listed in decreasing order based on the total number of introduced species found in each country): Lebanon (86 species), Greece (32), Italy (24), Turkey (20), Cyprus (13), Israel (eight), Spain (seven), Croatia (five), Malta (two), Libya (one), and France (one). Most likely, this pattern largely reflects the sampling bias due to unbalanced research effort in the different countries but also the unequal availability of marine caves per country. For example, Israel has a small extent of rocky coastline with caves, despite the high number of alien species reported from this country due to the proximity to the Suez Canal (Galil & Goren, 2019). On the other hand, the coastal zones of Turkey, Cyprus, and Malta contain many sea caves (Gerovasileiou & Bianchi, 2021), but they have not been yet extensively studied for their alien biodiversity (but see Öztürk, 2019). In Greece, recent surveys aimed at identifying introduced species in marine caves on islands of the South Aegean revealed more than 20 introduced species, including new records for this habitat type and Greek marine waters [e.g., the nudibranch *Plocamopherus ocellatus* Rüppell & Leuckart, 1828 and the decapod *Urocaridella pulchella* Yokes & Galil, 2006] (Katsanevakis *et al*., 2020a; Ragkousis *et al*., 2020, submitted; Digenis *et al*., 2021a, b, 2022a, b). The small number of introduced species in marine caves of Croatia and the Adriatic Sea (five species) could be partly attributed to the lower seawater temperatures (prohibitive for thermophilic alien species, as are most of the species introduced in the Mediterranean Sea) and the higher proportion of marine and anchialine caves with internal freshwater springs and stratified cold-water masses (Surić *et al*., 2010; Gerovasileiou *et al*., 2016).

Most introduced species were found at the entrance and in the semi-dark zone of shallow and/or semi-submerged caves (60 and 52 species, respectively), while only 19 species were found in the dark zone of caves. The introduced species that occur in the dark zone were: the hydrozoan *Clytia linearis* (Thorneley, 1900); the gastropod mollusc *Berthellina citrina* (Rüppell & Leuckart, 1828); the bivalve molluscs *Chama pacifica* Broderip, 1835, *Isognomon* cf. *australicus* (Reeve, 1858), *Malleus regula* (Forsskål in Niebuhr, 1775), and *Teredo navalis* Linnaeus, 1758; the polychaetes *Ficopomatus enigmaticus* (Fauvel, 1923) and *Notomastus aberans* Day, 1957; the amphipod *Jassa slatteryi* Conlan, 1990; the tanaidacean *Zeuxo coralensis* Sieg, 1980; the decapods *Carupa tenuipes* Dana, 1852 and *Urocaridella pulchella*; the cirriped *Balanus trigonus* Darwin, 1854; the bryozoan *Bugulina fulva* (Ryland, 1960); the ascidian *Herdmania momus* (Savigny, 1816); and the fish species *Enchelycore anatina* (Lowe, 1838), *Pempheris rhomboidea* Kossmann & Räuber, 1877, *Pterois miles*, and *Sargocentron rubrum* (Forsskål, 1775). However, many data sources lacked information on the distribution of species within caves and there was no such information for 34 species. However, most likely, these species were observed at the entrance or in the semi-dark zone of shallow and/or semi-submerged caves.

One possible explanation for the low number of introduced species reported from the dark zone of marine caves is that this confined and oligotrophic habitat limits – at least to some level – the establishment of some introduced species (Gerovasileiou *et al*., 2016; Bianchi *et al*., 2022). Nevertheless, some species can have a high abundance in sea caves, particularly motile species that conduct diel migrations. For example, a notable population explosion of the invasive Indo-Pacific sweeper fish *Pempheris rhomboidea* has been reported in marine caves of the eastern Mediterranean (Digenis *et al*., 2021a, 2022b).

Among the 126 introduced species recorded in Mediterranean marine caves, 67 (53.2%) are sessile, and 59 (46.8%) are motile. Most species (90: 71.4%) were found on hard substrates, and only seven on soft sediments (including two species found on both hard and soft substrates). The remaining species are benthopelagic (26) or pelagic (five). In addition, records for 14

molluscs (12 Gastropoda and 2 Bivalvia) were based on empty shells/thanatocoenoses found in cave sediment in Lebanon (Crocetta *et al*., 2013a, 2013b, 2020) and Cyprus (Di Franco *et al*., 2021) (Annex III - Supplementary material). These were the gastropods *Acteocina mucronata* (Philippi, 1849), *Biuve fulvipunctata* (Baba, 1938), *Cerithidium perparvulum* (R. B. Watson, 1886), *Cerithiopsis pulvis* (Issel, 1869), *Cerithiopsis tenthrenois* (Melvill, 1896), *Cingulina isseli* (Tryon, 1886), *Conomurex persicus* (Swainson, 1821), *Marmorofusus verrucosus* (Gmelin, 1791), *Miralda* sp. (reported as *Oscilla jocosa* Melvill, 1904 in Crocetta *et al*., 2020), *Pyrgulina pupaeformis* (Souverbie, 1865), *Pyrunculus fourierii* (Audouin, 1826), *Zafra selasphora* (Melvill & Standen, 1901), and the bivalves *Afrocardium richardi* (Audouin, 1826) and *Chama asperella* Lamarck, 1819. These records were not included in this update because it cannot be justified whether these species lived inside marine caves or if their empty shells were drifted there by currents or transferred by hermit crabs or predators such as octopuses (Gerovasileiou *et al*., 2016; Di Franco *et al*., 2021).

Native distribution range and pathways of introduction

The majority of introduced biota in Mediterranean marine caves (71% versus 62.5% in the previous census) originated from the Indo-Pacific Ocean, mainly from the Western and the Central Indo-Pacific biogeographic realms (Fig. 4 and Annex I - Supplementary material). Only 9.9% of the introduced species originated from the Atlantic Ocean (mainly from the Tropical Atlantic). Nine species had a circumtropical distribution. The native distribution range remains unknown for 15 species (cryptogenic). As expected, the contribution of species of Indo-Pacific origin to the introduced biodiversity increased from the western (47.4%) to the eastern (75.7%) Mediterranean (Fig. 4), in agreement with the previous census and general trends in the Mediterranean Sea (Gerovasileiou *et al*., 2016). The highest percentage of introduced Atlantic and circumtropical species (13.9% and 16.7%, respectively) was found in the central Mediterranean, while the highest contribution of species of unknown origin was found in the Adriatic Sea and the western Mediterranean (60% and 36.8%, respectively) (Fig. 4).

We assume that most introduced species have entered marine caves from neighbouring habitats outside caves, unaided. The possibility that some species might have reached semi-submerged caves through tourist boats that visit sea caves in high numbers, especially during the warmest summer months, cannot be ruled out (Gerovasileiou *et al*., 2016). When examining the original pathway of all species in the Mediterranean Sea (Fig. 5), it appears that the majority (60.7%) have entered the basin through the Suez Canal – the so-called Lessepsian species – (pathway: Corridors) followed by vessel transferred species (34.6%) (pathway: Transport-Stowaway). All other pathways accounted for much smaller percentages, specifically 2.8% for Transport-Contaminant, 1.6% for Escape from confinement, and 0.3% for Release in nature. As depicted in Figure 5, the Lessepsian migrants dominate in the marine caves of the eastern Mediterranean, spread and invade caves in the central and reach even the western Mediterranean, but are absent (or at least not discovered to date) from caves of the Adriatic Sea. On the other hand, vessel-transferred alien species are present in sea caves in all Mediterranean regions, particularly in the eastern Mediterranean, less so in the Adriatic.

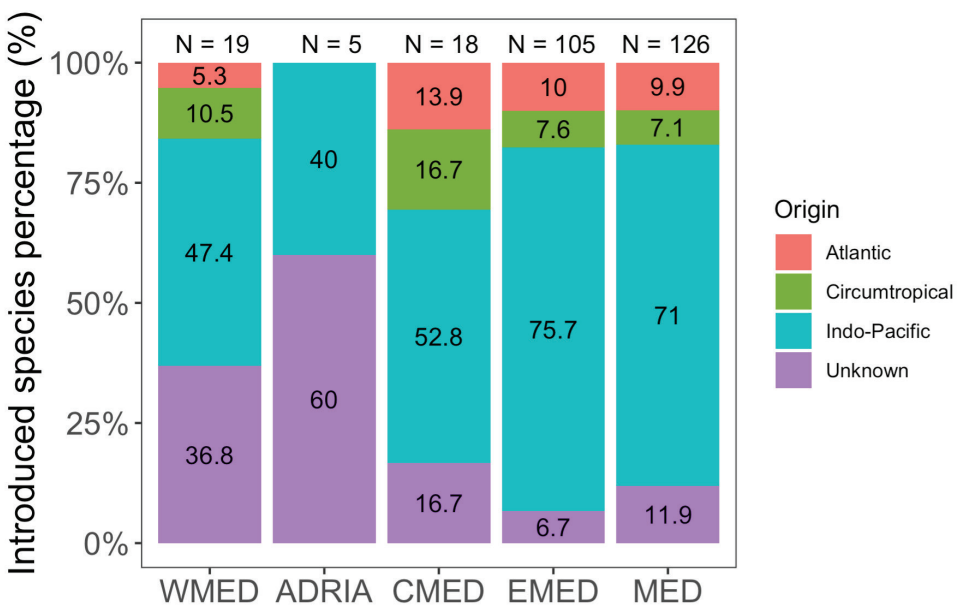

Fig. 4: Percentage of introduced biota reported from marine caves by origin (native distribution range) in different Mediterranean regions: WMED = Western Mediterranean; ADRIA = Adriatic; CMED = Central Mediterranean; EMED = Eastern Mediterranean; MED: Mediterranean Sea (all regions). When the native distribution range of a given species included both the Atlantic and Indo-Pacific, the analysis considered them both giving equal weight to each ocean, so that the total sum of weights per species equals one.

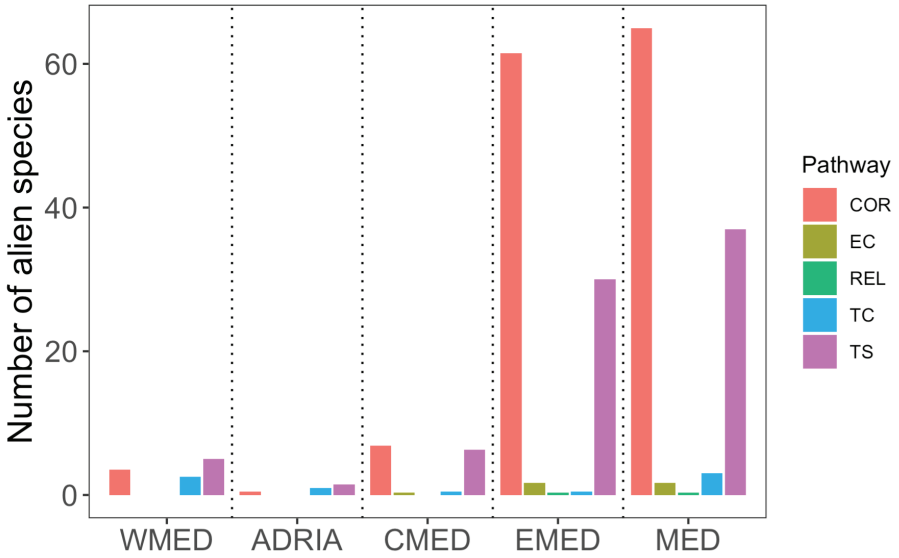

Fig. 5: Pathways of introduction of alien species reported from marine caves in the Mediterranean Sea by different MSFD regions: WMED = Western Mediterranean; ADRIA = Adriatic; CMED = Central Mediterranean; EMED = Eastern Mediterranean. When more than one pathway of introduction was suspected or documented for a given species, the analysis considered them all giving equal weight to each pathway, so that the total sum of weights per species equals one. COR = Corridor; REL = Release in nature; EC = Escape from confinement; TC = Transport-Contaminant; TS = Transport-Stowaway.

Impact of introduced species

Approximately 28% of the introduced species (35 species) found in marine caves have a high impact on marine ecosystems (based on EASIN data). In addition, nine out of the ten worst invasive species found in the Mediterranean Sea, as ranked by Tsirintanis *et al*. (2022) based on their negative impact score (accounting only for impacts on biodiversity), have been recorded in marine caves. These are (listed from higher to lower impact score): *Caulerpa cylindracea* Sonder, *Womersleyella setacea* (Hollenberg) R. E. Norris, *Lophocladia lallemandii* (Montagne) F. Schmitz, *Brachidontes pharaonis* (P. Fischer, 1870), *Siganus luridus* (Rüppell, 1829), *Rugulopteryx okamurae* (E. Y. Dawson) I. K. Hwang, W. J. Lee & H. S. Kim, *Siganus rivulatus* Forsskål & Niebuhr, 1775, *Acrothamnion preissii* (Sonder) E. M. Wollaston and *Spondylus spinosus* Schreibers, 1793. Six of these species have been found only at cave entrances (five are macroalgae), two have been found only in semi-dark cave sections (*B. pharaonis* and *S. spinosus*), and one has been found in both zones (*S. luridus*). To our best knowledge, there is no data on the impacts of introduced species on marine cave biodiversity to date. The lack of data series regarding the past ecological state of most Mediterranean marine caves – especially from the understudied eastern Mediterranean Sea – hinders such an assessment. Crocetta *et al*. (2013a) compared recent and historical data on the mollusc diversity of Lebanon from various habitat types (including sea caves); they found that many habitat-forming bivalves, which were common in the past, have probably been replaced by the alien bivalves *Brachidontes pharaonis*, *Chama pacifica*, and *Spondylus spinosus*.

In addition, during the last years, three highly invasive fish species have become very common – often in high abundance – in marine caves (in all cave zones) of the south-eastern Mediterranean Sea (Annex I - Supplementary material and personal observations by VG), constituting a potential threat that should be further investigated and monitored. These are the lionfish *Pterois miles*, the sweeper fish *Pempheris rhomboidea*, and the red squirrelfish *Sargocentron rubrum* (all of Indo-Pacific origin). *Pterois miles* is a voracious opportunistic predator that has the potential to significantly affect food webs in Mediterranean ecosystems by preying on a variety of fish and secondarily on invertebrates (including cave crustaceans: Jimenez *et al*., 2019), competing with native consumers (Tsirintanis *et al*., 2022 and references therein). *Pempheris rhomboidea* and *S. rubrum* hide inside caves and crevices of the seabed during the daytime and move out from their shelters at night to feed. These diel movements (in high aggregations for the species *P. rhomboidea*) could potentially affect the oligotrophic marine cave ecosystem (especially the confined dark cave sections) by increasing the flow of organic matter (through metabolic excretion) from the external environment (Gerovasileiou *et al*., 2016; Bussotti *et al*., 2018). In addition, these species could compete for space and resources with native fish occupying the same habitats, such as the cardinalfish *Apogon imberbis* (Linnaeus, 1758) (Tsirintanis *et al*., 2022 and references therein). Recent surveys with visual census in marine caves of the South Aegean Sea showed that *P. rhomboidea* reached considerably high abundances (> 200 individuals at the dark interior and more than 200 juveniles at the entrance) in a semi-submerged cave in Kastellorizo Island (Greece), comprising 46% of all recorded fish individuals (Digenis *et al*., 2021a). Unfortunately, the absence of previous data from the same cave does not allow for the evaluation of changes in the structure of fish assemblages or the ecological state of the marine cave ecosystem.

Concluding remarks and future perspectives

This update of introduced species in Mediterranean marine caves showed that their number has significantly increased (2.2 times higher) within eight years from the previous census (Gerovasileiou *et al*., 2016). In addition to augmented scientific effort, this increase is in line with the reported establishment rate of new marine alien species in the Mediterranean Sea; Zenetos *et al*. (2022b) documented a 40% rate in establishment success of biological invaders in the Mediterranean in the period 2011-2021, 13% of which took place in the last two years (2020-2021). Regional and spatial distribution patterns, as well as trends regarding native distribution range and possible pathways of introduction, have not changed, except for a higher contribution of Indo-Pacific species, presumably through Lessepsian migration, and additional data on the population explosion of some fish species. However, the actual number of introduced species in marine caves is probably much higher, given the limited research effort regarding inconspicuous small-sized taxa (e.g., sessile invertebrates and soft-substrate taxa), specifically in the eastern and central Mediterranean, where numerous marine caves and introduced species occur (Gerovasileiou *et al*., 2016; Gerovasileiou & Bianchi, 2021). Therefore, marine caves should be urgently considered in existing and future monitoring networks to assess their current ecological state (as a baseline for future comparisons) and identify imminent threats, including introduced species. The adoption of eDNA approaches (e.g., Obst *et al*., 2020) should also be considered, as an early warning tool, especially for inconspicuous taxa. Species that are known to occur in sea caves of adjacent marine areas (e.g., Western Indo-Pacific and Tropical Atlantic) could represent future newcomers to this habitat type in the Mediterranean Sea, although it remains unknown whether sea caves could be used as "stepping stones" for their expansion (Gerovasileiou *et al*., 2016; Digenis *et al*., 2022a). For instance, the cardinalfish *Apogonichthyoides pharaonis* (Bellotti, 1874), which was identified as a potential future newcomer in the previous census due to its preference for cryptic habitats in its native distribution range (Gerovasileiou *et al*., 2016), was indeed recorded in marine caves of Lebanon (Zenetos *et al*., 2015b), Israel (Galil & Goren, 2019), and, more recently, Greece (Ragkousis *et al*., submitted). In addition, the development of experimental approaches and comparisons between "invaded" and "not invaded" sea caves are needed to investigate the potential effects of introduced species on the marine cave ecosystem and its fragile biodiversity.

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Supplementary Material

The following supplementary information is available online for the article:

Annex I. Checklist of introduced species reported from Mediterranean marine caves accompanied with data on taxonomic classification (according to WoRMS), alien status, native distribution range (origin), pathway of introduction in the Mediterranean Sea, impact on native biodiversity, spatial distribution in the Mediterranean Sea (by ecoregion, MSFD region and country) and within marine caves (cave zone), mobility, habitat/substrate, and source of information (references - see Annex II).
Annex II. List of references for records of introduced species from Mediterranean marine caves cited in Annex I.
Annex III. Checklist of introduced molluscs reported from marine caves based only on empty shells/thanatocoenoses (for references see Annex II).